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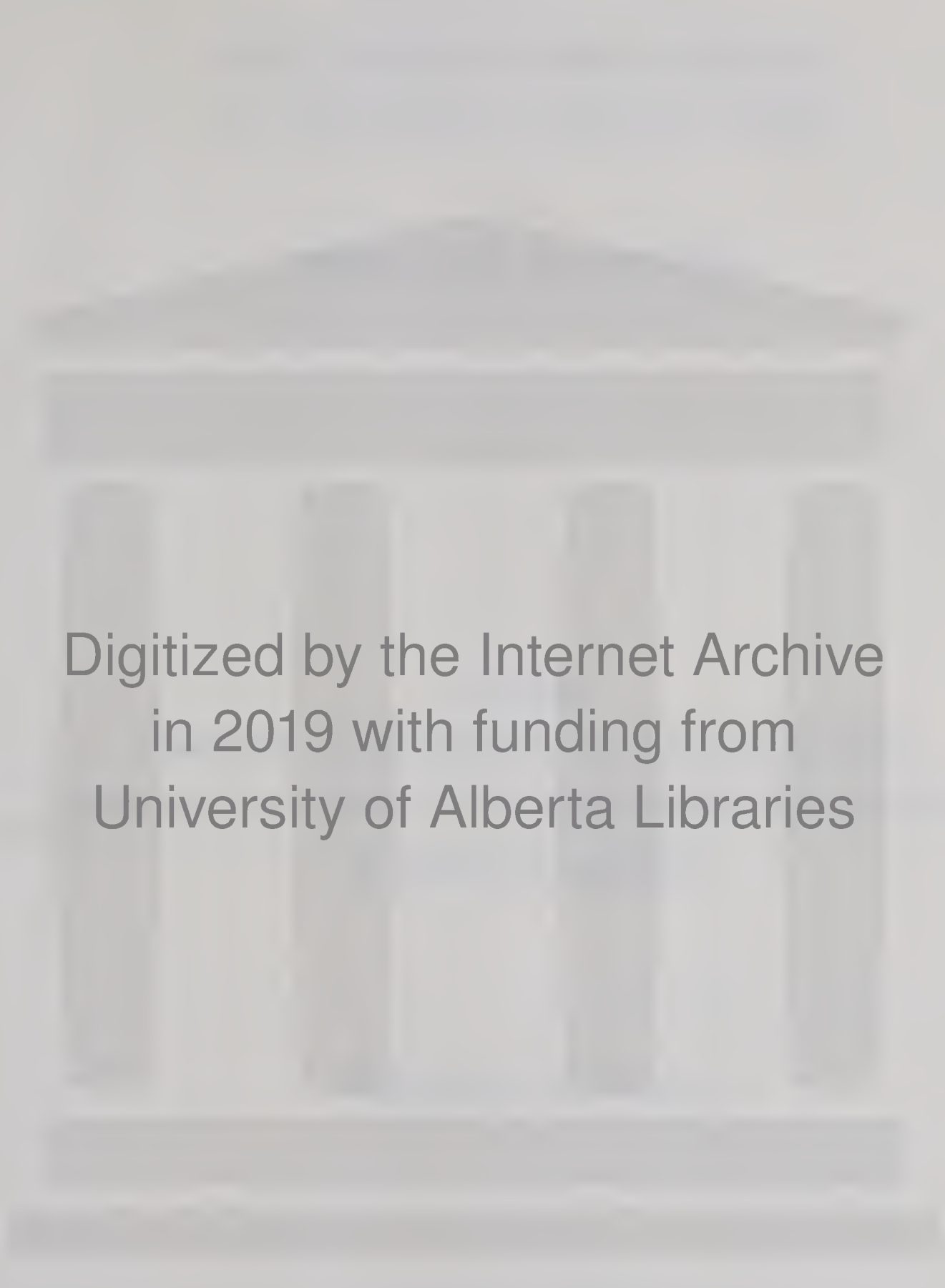
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LIGHT ALTERATION CAUSED BY SNOW AND
ITS IMPORTANCE TO SUBNIVEAN RODENTS.

by

LORNE LESLIE NEIL EVERNDEN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
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OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

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UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled Light Alteration Caused by Snow and Its Importance to Subnivean Rodents submitted by Lorne Leslie Neil Evernden in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

An attempt was made in this study to examine the effect of a meteorological phenomenon, snow, on a physical environmental factor known to be of physiological importance to mammals, namely light.

By the use of selenium cells placed in various environmental areas prior to snowfall, it was discovered that light levels in the subnivean environment decrease proportionately to the amount of snow cover. Under 15 cm of snow in the fall, light levels were reduced to very low levels. Mid-winter snow depths of 30 to 50 cm reduced light to levels undetectable by the selenium cells used. Thus it appears that the subnivean environment is one of almost total darkness. It was also discovered that those light rays which do penetrate to ground level are mainly long wave length (red) rays, to which the voles studied, Clethrionomys gapperi, appear to be insensitive.

Laboratory experiments with C. gapperi suggest strongly that the females of this species are sensitive to white and blue radiation. They also become capable of breeding earlier than normal if exposed to increased day length during late winter. Red light was not stimulatory, regardless of the long photoperiod. Low temperatures did not prevent animals from responding to increased photoperiod with white light. As in other mammalian species studied, male voles did not appear to be as strongly photosensitive as the females.

It is suggested that, in northern latitudes where the

increase in light intensity and photoperiod are in essence controlled by snow depth rather than the angle of incidence of sunlight, unusual decreases in snow depth during the winter might simulate the increasing day length of spring. This could result in the phenomenon of winter breeding. Similarly, an early snow melt in the spring might result in earlier-than-normal breeding and consequently in the production of greater numbers of offspring in that particular year. Both of these events might contribute significantly to the fluctuations from year to year in microtine numbers.

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I must also express my thanks to the many colleagues and faculty members who offered their services and opinions for my benefit, most notably Mr. David Aiken, Mrs. Vi Scott, Dr. S. E. Zalik, Prof. R. W. Longley, Dr. C. Hampson, and Dr. P. Hallett.

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"A meadow mouse, startled by my approach, darts damply across the skunk track. Why is he abroad in daylight? Probably because he feels grieved about the thaw. Today his maze of secret tunnels, laboriously chewed through the matted grass under the snow, are tunnels no more, but only paths exposed to the public view and ridicule. Indeed the thawing sun has mocked the basic premises of the microtine economic system!

"The mouse is a sober citizen who knows that grass grows in order that mice may store it as underground haystacks, and that snow falls in order that mice may build subways from stack to stack: supply, demand, and transport all neatly organized. To the mouse, snow means freedom from want and fear."

Aldo Leopold

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INTRODUCTION

Attempts have been made to delineate the physical environmental factors which are of prime importance to mammalian reproduction. The two factors which received the most attention are light and temperature.

It would be at least foolish and probably erroneous to attempt to single out either of these factors as the one most important to reproductive success in any one animal species. Almost certainly both are involved to a greater or lesser degree, depending on the particular circumstances. And, as these factors are of importance to mammalian reproduction, it follows that any meteorological element which alters their effect on the animal shares this importance. It is with one such secondary or modifying factor that this study is concerned.

In retrospect, it is strange that an environmental parameter as evident as snow could be nearly ignored by western biologists, yet this has been the case. In recent years, some research into the importance of snow has been published by Pruitt (1957, 1960). Pruitt has confirmed Formozov's contention (1963) that the subnivean environment is one of considerable stability and relative comfort. The rodents and insectivores inhabiting it are faced with an amazingly constant temperature of just below freezing, allowing survival of mammals too small in mass to withstand the severe temperatures of a northern winter. In addition, this environment contains a variety of foodstuffs and excludes

most predators. Pruitt concludes that the presence of snow cover is essential for the continued success of small northern mammals.

Dunaeva (1948), Koshkina (1957) and Fuller (unpubl. ms.) have cautioned against regarding the presence of snow as being entirely beneficial. They point out that a slow, wet spring brought about by fluctuating temperatures may cause considerable stress and mortality to subnivean occupants. Therefore, for a sizable breeding population to emerge in the spring, it may be necessary to have a spring of gradually rising temperatures and consequent sublimation of snow (as opposed to melting). Under these conditions, the animals will be faced with a dry environment immediately upon disappearance of the snow cover.

All studies to date on the modifying effect of snow cover and its consequent importance to small mammals have dealt with temperature. The present study was designed to initiate studies on the effect of snow on another important physical factor, light.

If in fact snow alters the passage of light, then any effect wrought by this factor on the animal may be actually under the control of snow. This study was undertaken primarily to examine this possibility, as well as to contribute to the already large quantity of literature on mammalian photosensitivity by experimenting with yet another microtine species, Clethrionomys gapperi.

IMPORTANCE OF LIGHT

Awareness of the role of light in the annual breeding cycles stems from the pioneering work of Wm. Rowan (1925), who demonstrated gonad development in Juncos exposed to increasing day length in the dead of winter. This sparked a great deal of research into the effect of light on birds, but inquiries into the effects on other groups of animals were somewhat slower in coming.

Second only to avian research, the greatest amount of attention has been paid to the response of mammals to light. Initial inquiries were made by Baker and Ransom (1932), who observed almost complete failure of reproduction in the field mouse (Microtus agrestis) when the daily light period was reduced from 15 to 9 hours. At about the same time, Bissonette (1932) reported the appearance of oestrus in ferrets in November and December, a full 4 months ahead of normal, following the addition of 6 hours of light to the normal daily photoperiod from 12 October on.

Researchers following Baker and Ransom's lead have confirmed the effect of light for several other voles and mice (Cowan and Arsenault, 1954; Frank, 1956; Pinter and Negus, 1965; Lecyk, 1962; Whitaker, 1936). Those following in Bissonette's track have elaborated considerably on the effects of light on ferrets, probably because the size of this animal better suits it to physiological research.

The repetition of Bissonette's initial work gave similar results (Allanson, Rowlands and Parkes, 1934; Bissonette,

1936, 1938; Clark, McKeown and Zuckerman, 1937; Hill and Parkes, 1933). Later work suggests that the primary effect is through the eye (Thompson, 1950, 1954; Bissonette, 1935; Clark, Leonard and Bump, 1937; Jefferson, 1940). Another dimension was added by Marshall and Bowden (1934, 1936) and Marshall (1940) who demonstrated that the response of the ferret to light varies directly with intensity and that there is a differential response to wave length. Ultra-violet radiation produced the greatest response and infra-red the least. (Results for specific colors in between these extremes were variable, but these results are complicated by intensity differences).

While the majority of mammalian work has been done on voles and ferrets, many others have also been tested. Hammond (1954), in his review article on the effect of light on mammals, cites references demonstrating that the following are capable of responding to the stimulus of light: deer, fox, fur seal, goat, hedgehog, horse, long-tailed weasel, marmoset, mink, pine marten, rabbit, raccoon, rat, and sheep.

It would appear then that light is commonly a factor in stimulating the onset of breeding in mammals as well as in birds. However, the mechanisms by which this control is exercised are still open to considerable speculation.

While the dependence of the gonads on the adenohypophysis

has been recognized for some time (Smith and Engle, 1927), it was left for Marshall (1942) to fully realize and state the dependence of the pituitary and hence the gonads on the nervous system, so that "the endocrine rhythm of the sexual cycle is constantly liable to modification through exteroceptive factors (whether sexual or otherwise environmental), acting through the agency of the central nervous system (and probably through the hypothalamus) upon the anterior pituitary gland, the secretory functions of which vary according to the stimuli which the organ receives". At this point the awareness of the dependence of endocrine functions on the brain lent increased understanding to why and how light, which Rowan had already demonstrated to be of importance, could in fact mediate a response. Attempts to clarify the pathways have been only partially successful (Critchlow, 1963; Thompson and Zuckerman, 1954; Clark, McKeown and Zuckerman, 1937). It is clear, however, that the pituitary must be involved in gonad development, and hence light must somehow affect the pituitary through the central nervous system. In mammals, almost the total light response is through the eye (Van Brunt et al., 1964), while in the thinner-skulled birds, there seems to be some extra-retinal sensitivity (Benoit, 1964). Even in the mammal, however, the fact of excessive sensitivity to ultra-violet suggests that more than the normal retinal elements may be involved (and hence, more than just visible wave lengths may be effective).

While exact delineation of the effect of light on the

adenohypophysis remains to be studied, another means of effecting gonadal response in mammals is presently being elucidated. For some time now it has been apparent that the pineal gland is in some way involved in the light response in mammals (Fiske et al., 1960; Gardner, 1953; Kappers, Huber and Crosby, 1936; Kitay and Altschule, 1954; Quay, 1956). Only recently have Wurtman and Axelrod (1965) published a synthesis of results demonstrating that the pineal produces an anti-gonadotropin which, while present, prevents any response of the rat to increased illumination. Extirpation of the pineal results in immediate sexual development, and premature sexual development in humans has been explained through pineal damage. The size of the pineal decreases with increased exposure of the rat to light, suggesting that the synthesis of the anti-gonadotropin by the pineal is itself inhibited by the effect of light received on the retina.

The realization of the importance of the pineal and the effect of light on it greatly enhances our understanding of how light may modify sexual development in natural populations. Belief has often been expressed (though not conclusively proven) that mammals possess an inherent rhythm which will cause them to come into breeding condition at roughly the same time each year, and that light and other external factors serve to synchronize this internal clock with the external conditions. The pineal mechanism explains admirably how this modification may be accomplished, but presupposes that the animal is capable of developing before hand (i.e., pituitary gland is producing FSH).

It seems clear that mammals possess the necessary physiological equipment to utilize light as a stimulant to spring (or fall) breeding. This belief is confirmed by the large number of mammals known to respond to light. But the question remains as to whether weather conditions in spring might cause a delay in the information (increasing day length) reaching the animal and hence a delay in breeding.

STUDY AREA

All field work was done within a 2-mile radius of Ellerslie, Alberta, which is about 7 miles south of Edmonton (Lat. 53° , $30'N$; Long. 113° , $45'W$). The main part of the study was done on the property of Dr. Cyril Hampson, 2 miles west of Ellerslie. Constantly operating subnivean light meters were located here, while the sampling of natural populations was done in a large spruce bog one half mile south of Dr. Hampson's property.

Samples of color temperature and light intensity through snow profiles were taken throughout the study area.

All laboratory work was done on the premises of the Department of Zoology at the Edmonton campus of the University of Alberta.

Figure 1. Station #1 (open clearing). General view.

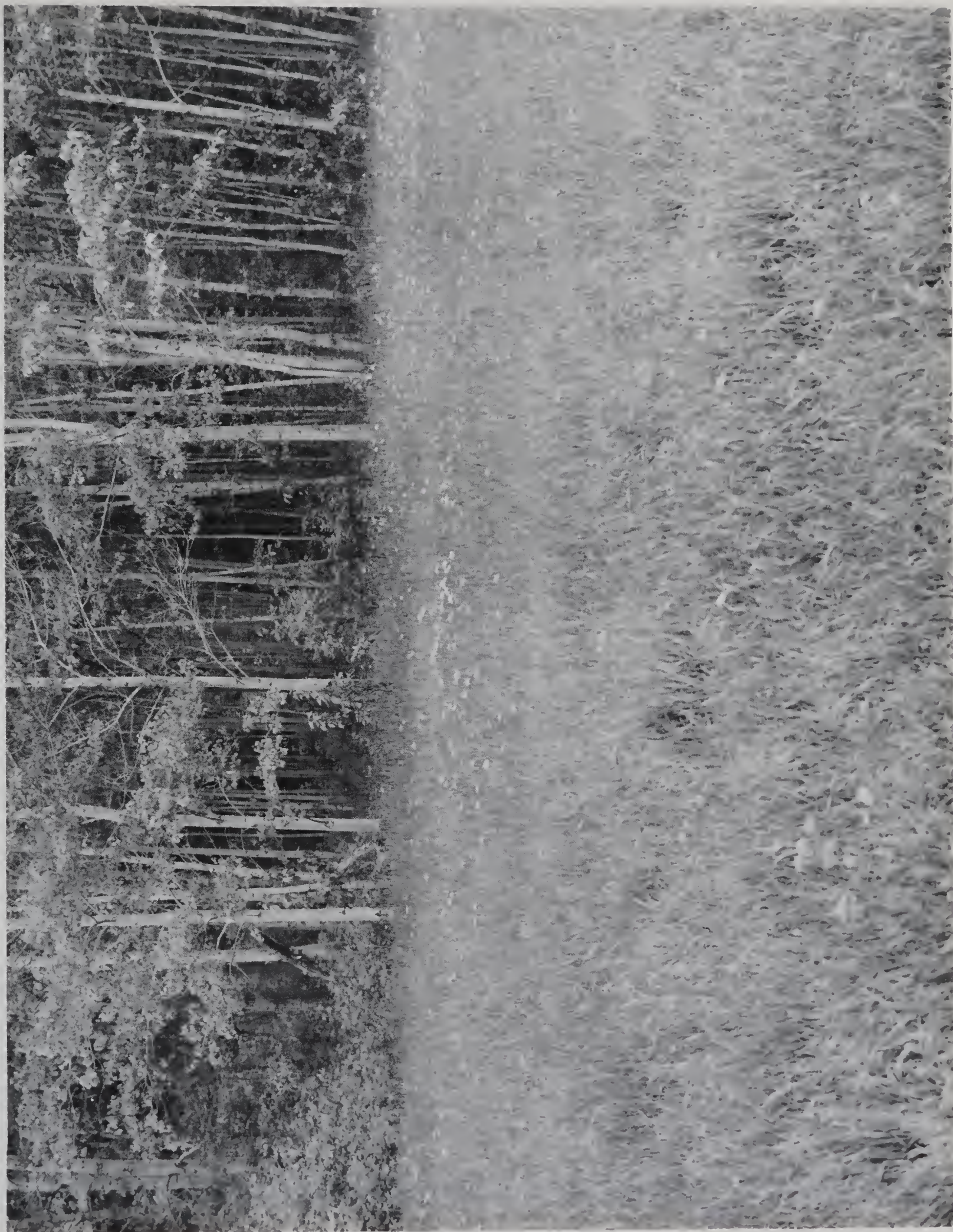


Figure 2. Station #1 (open clearing). Specific location of selenium cell.



Figure 3. Station #2 (poplar forest). General view.



Figure 4. Station #2 (poplar forest). Specific location of selenium cell.



Figure 5. Station #3 (spruce forest). General view.



Figure 6. Station #3 (spruce forest). Specific location of selenium cell.



MATERIALS AND METHODS

ENVIRONMENTAL LIGHT RECORDINGS

Intensity and Photoperiod

Records of light intensity were taken continuously from 20 November, 1965 through 7 April, 1966 at three stations under the snow. The three recording stations were located in three different types of habitat; open clearing, poplar forest, and spruce forest (Fig. 1 to Fig. 6 incl.).

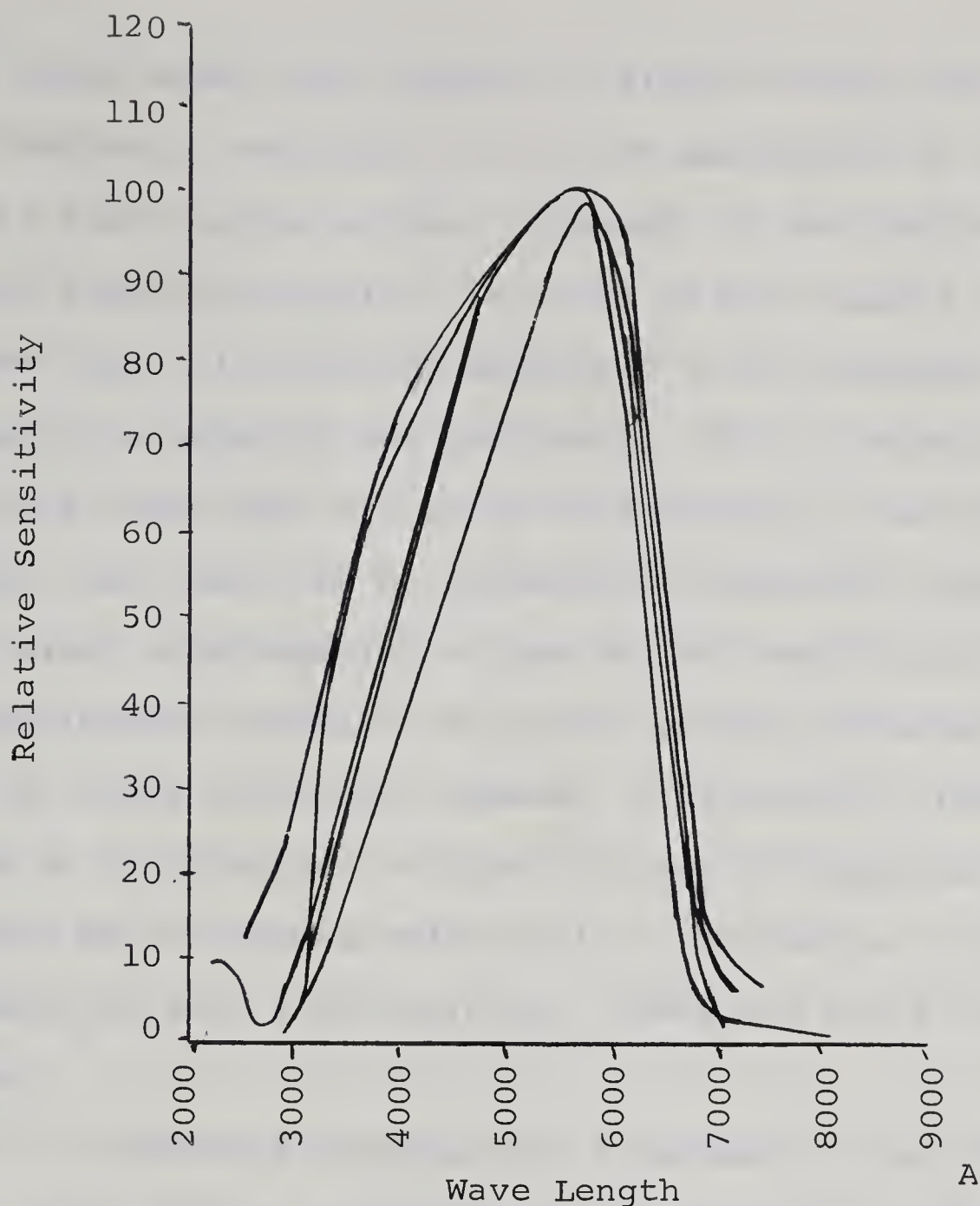
Similar recordings were made available to me by Mr. David Aiken, whose interests require that he keep constant light recordings above the snow. Rather less complete light records were also available through the Meteorological Branch of the Department of Transport at the Edmonton International Airport (located about five miles south of the study area).

Before the first fall of snow in November, 1965, selenium light-sensitive cells (International Rectifier Company, El Segundo, California, U.S.A., model S4M - P2) were laid down at each station, with leads running to a nearby building which housed three Rustrak Model 88 recorders.

Following the first snowfall, these recorders were activated and were left operating continuously to measure the current generated by the light cells in milliamperes. The open air light station operated by Mr. Aiken was similar, but used a somewhat less sensitive selenium cell. It was located on the roof of the Agriculture and Biological Sciences Building at the Edmonton Campus of the University of Alberta, seven miles north of the study area.

When data acquired from a light cell are to be used to estimate the light available to an animal in a similar environment, it is essential that one understand the nature of the photocell and how its response may differ from that of the eye. The selenium type of photocell, used in this study, is probably the best choice for zoological work since its wavelength sensitivity spectrum is quite similar to that of the human eye. (For estimation of the sensitivities of other vertebrate eyes the reader is referred to Pirenne (1956).) Like the human eye, the selenium cell is more sensitive to some wave lengths than to others (maximum sensitivity at 5900 A), but it is more sensitive than the eye to both ends of the visible spectrum (i.e., a red or violet source would be rated as a higher intensity by the photocell than by the eye). Donaldson (1958) diagrams the sensitivity curves of several selenium cells. His graph is roughly reconstructed below.

Donaldson also claims that, given a small external resistance as was the case in this study (100 ohms), only very small inaccuracies (<1%) will arise from using the cells at low temperatures. Being located under the snow, the photocells in this study were operating at about the freezing point of water.



Spectral response of various selenium barrier-layer cells of American manufacture. (Donaldson, P. E. K., 1958).

Another consideration about the nature of the photocells arises in respect to the presentation of the light data. The recorders show light intensity as milliamperes of energy output by the photocells. The question arises whether one should attempt to convert these values into one of the more conventional light units, such as lux or foot-candles. However, these units have meaning only with respect to human foveal vision and at fairly high intensities. When speaking in terms of a selenium cell with characteristics not identical with human foveal vision, and especially with a cell operating

in dim light under wave lengths of light to which the cell is not maximally sensitive, it is not meaningful at all to speak of foot-candles or lux. Instead, it was decided that to avoid misinterpretation, it would be most useful to deal with the light fluctuations expressed in milliamperes, as originally recorded by the photocell. This is especially true since these data are to be used primarily for comparative purposes, and could not be converted to absolute values without an exact understanding of the retinal sensitivity of the experimental animals. To give a crude indication of the levels of light concerned, however, a calibration from milliamperes to foot-candles and lux is given in Appendix 3. It cannot be overemphasized that it is erroneous to put too much faith in such a calibration. Aiken and Poole (1937a) caution:

....readings obtained are a measure of the electric current generated by the energy falling on the sensitive surface of the cell. The measurement does not give the illumination, unless carried out after a careful examination of the properties of the cell and with due regard to the optical conditions under which the light reaches it.

Although it is recommended that an opal diffusing glass be placed over each photocell to avoid reflections, this was not followed in the present study. Use of such a diffusor cuts the sensitivity of the cell by 45 per cent which would be an extreme handicap when recording subnivean light. It

was also felt that the snow cover itself would act as a sort of diffuser.

In addition to the three light meters described above, which were intended to indicate variations in light present as the snow cover increased, and to estimate total photoperiod in the subnivean environment, recordings were taken through snow profiles at regular intervals during the winter by a method similar to that described below under "color temperature". A Weston Mark IV light meter (Weston Instruments Inc., Newark, New Jersey, U.S.A.) was used for these readings, which were, of necessity, taken in foot-candles. The reader is again cautioned against regarding this as an absolute unit.

Data from the continuously operating light meters were summarized to hourly readings and photoperiod. It was decided that the most meaningful way to describe total illumination was to total hourly milliamperere readings, thus obtaining a crude estimate to total area under the curve on the Rustrak recording. This method illustrates the changes which occurred in daily illumination. However, this technique also has the disadvantage of confusing two distinct variables, photoperiod and intensity. While photoperiod was dealt with separately, there is the possibility that in totaling intensity readings throughout the day, one might distort the results such that a long day of low intensity might appear greater than a shorter day with high intensity. However, since results clearly show decreases in illumination after the shortest day of the year, it is clear that the problem was not serious

in this case, and it was decided that the units given are a fair indication of the actual changes in intensity which occurred.

Color Temperature

Readings of color temperature through snow profiles were taken at regular intervals throughout the winter and spring with a Gossen Sixticolor Color Temperature Meter (Kling Photo Corporation, 257 Park Ave. S., New York, N.Y.). This instrument is designed for photographic use and gives limited direct information about the exact spectral composition of the light reaching it. It does, however, give an indication of the proportions in which several colors are present. Readings are given in degrees Kelvin, referring to the spectral characteristics of radiation emitted by a black body at that temperature. A low reading indicates a preponderance of light in the red end of the spectrum, and with increasing color temperature, a greater amount of the shorter blue-violet radiation is suggested. The color temperature meter was checked under very dim illumination in the laboratory to make certain the meter would not read inaccurately under low light intensities.

Readings were taken by first digging a trench in the field of snow; next, a small hole was dug into the exposed wall of snow; the meter was then inserted and pressed upward so as to bury it in the snow in such a way that no side light would reach it. As an added precaution, the side was covered as much as possible by the author's body before the reading was taken. A reference reading was then taken above the

snow. Depth of snow above the meter when the reading was taken, a brief description of the surrounding habitat, and any outstanding characteristics of the snow were noted.

ADDITIONAL WEATHER DATA

Records were kept of the depth of snow above each of the subnivean light cells at intervals of three or four days. Records of total radiation (in Langleys) and of subnivean temperatures were made available to me by Prof. Longley of the University of Alberta, Department of Geography, who operates a small weather unit only a few hundred yards from my study area. Official records of daily snowfall, standing snow depth, hours of bright sunlight, and mean daily temperature at the Edmonton International Airport were obtained from the Meteorological Branch of the Department of Transport.

TRAPPING

Live Trapping

Live trapping was accomplished during the first week of February, using Sherman traps which were insulated by wrapping them with terylene fibre and then covering them with polyethylene. Terylene nesting material was provided, but no bait was used. With this apparatus, trap mortality was low, even though traps were checked only morning and evening. Air temperatures were moderate during this period, averaging about 10 F.

While a larger sample of animals could have been obtained by fall trapping, it was considered essential that the animals be left under field conditions until it was actually time to perform the lighting experiments, since facilities were not available to maintain winter temperatures and natural foods in the laboratory, and since the object was to speed spring breeding, not to induce winter breeding. In this way it was hoped that the effects of these two factors could be minimized.

Additional live trapping was done in early May for animals to be used in color preference experiments.

Snap Trapping

Snap trapping was done regularly at approximately 3-day intervals commencing in mid-March and continuing through April and May until pregnant animals were obtained. The intent of this operation was to record the onset of breeding in the wild population from the study area. Clethrionomys gapperi were found in large numbers throughout the entire study.

Animals so trapped were weighed, measured, and autopsied. Testis weights were taken in the males, and these organs, along with the epididymides and seminal vesicles were preserved in Bouin's solution. Histological examination was carried out later to provide information on the rate of development.

In females, the ovaries and oviducts were weighed and preserved in Bouin's for later histological examination.

Since only Clethrionomys gapperi was to be used in the laboratory studies, snap traps were set in locations deemed likely habitat for this species. However, Peromyscus maniculatus and Microtus pennsylvanicus were occasionally captured and were autopsied and measured in the same way as C. gapperi.

HISTOLOGICAL EXAMINATION OF WILD SAMPLES

After fixation, reproductive organs from both laboratory and wild populations were sectioned at 10 microns, and stained with Heidenheins Hematoxylin (males) or rapid Mallory (females).

The testes of all laboratory males, and of two males from each trapping date in wild populations, were examined histologically. Developmental stages were characterized as follows, and each animal so rated:

- I no development (i.e., tubules closely packed, lumen closed, no sperm visible). (Fig. 7)
- II..... slight development (tubules slightly less closely packed than in (I), lumen small, spermatids visible around lumen, very few sperm visible). (Fig. 7)

- III.... full (lumen very obvious, considerable quantities of sperm visible in the lumen of the tubules). (Fig. 8)
- IV..... very full (tubules contain large masses of mature sperm). (Fig. 8)

In assigning a stage to a particular animal, a large number of sections were surveyed and evaluated. The classification given is a subjective evaluation of the overall degree of development of the testis.

All females from both laboratory and wild populations were examined histologically. The ovaries of laboratory animals were serially sectioned, while those from the wild animals were sectioned at two levels through the middle of the gonad.

Females were graded from one to five depending on the following structures:

- 0 no development of follicles
- I primary follicles only
- II..... growing follicles present, usually in addition to primary follicles (graded as in Romer, 1962).
- III.... maturing follicles present, usually in addition to primary and growing follicles (graded as in Romer, 1962).
- IV..... mature Graafian follicles present, usually in addition to all preceeding stages.
- V corpora lutea present, usually in addition to many or all of the above developmental stages.

While the stages observed were classified according to

Figure 7. Degree of testicular development:

Stage 1 - no sperm visible.

Stage 2 - spermatids and a few sperm visible.

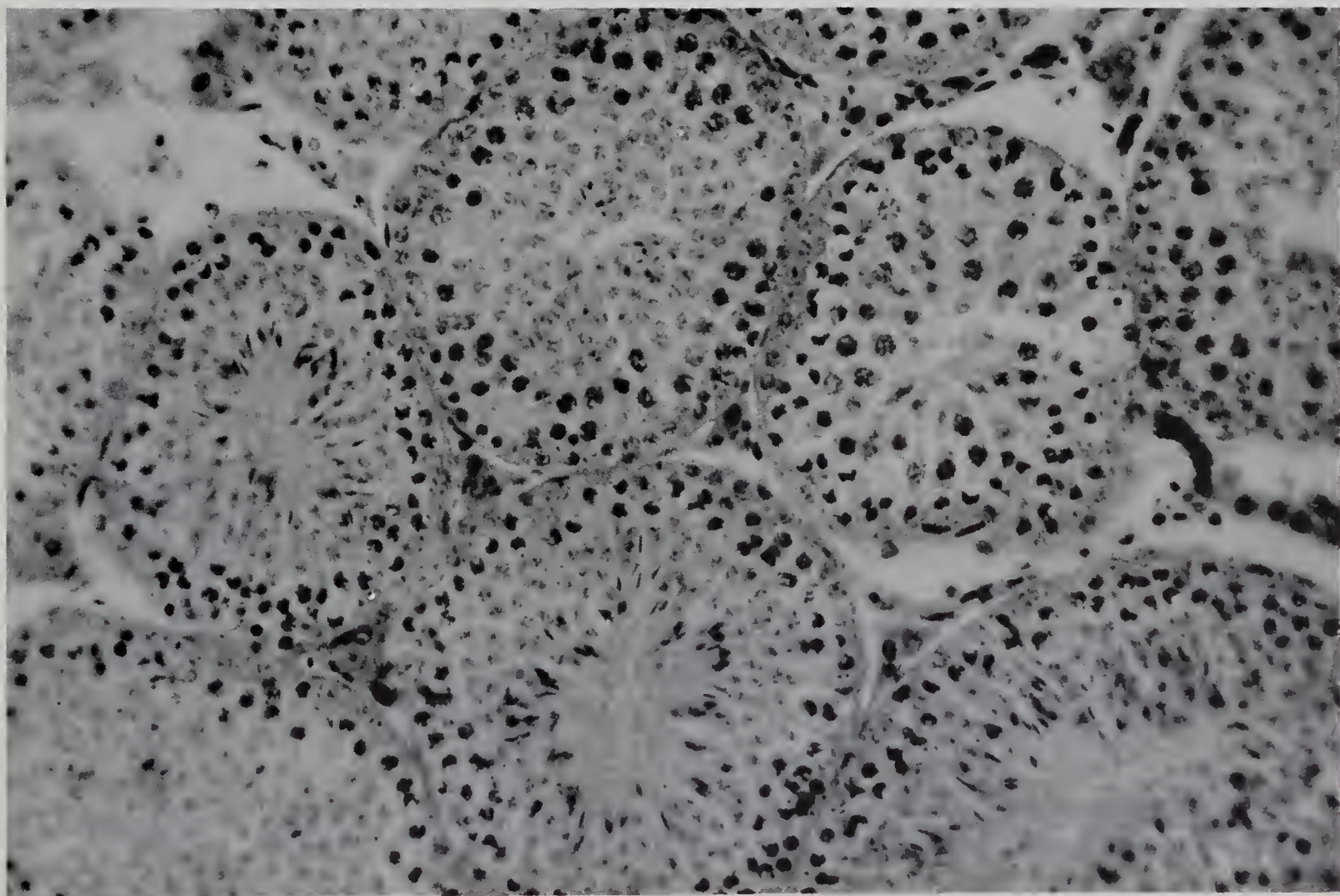
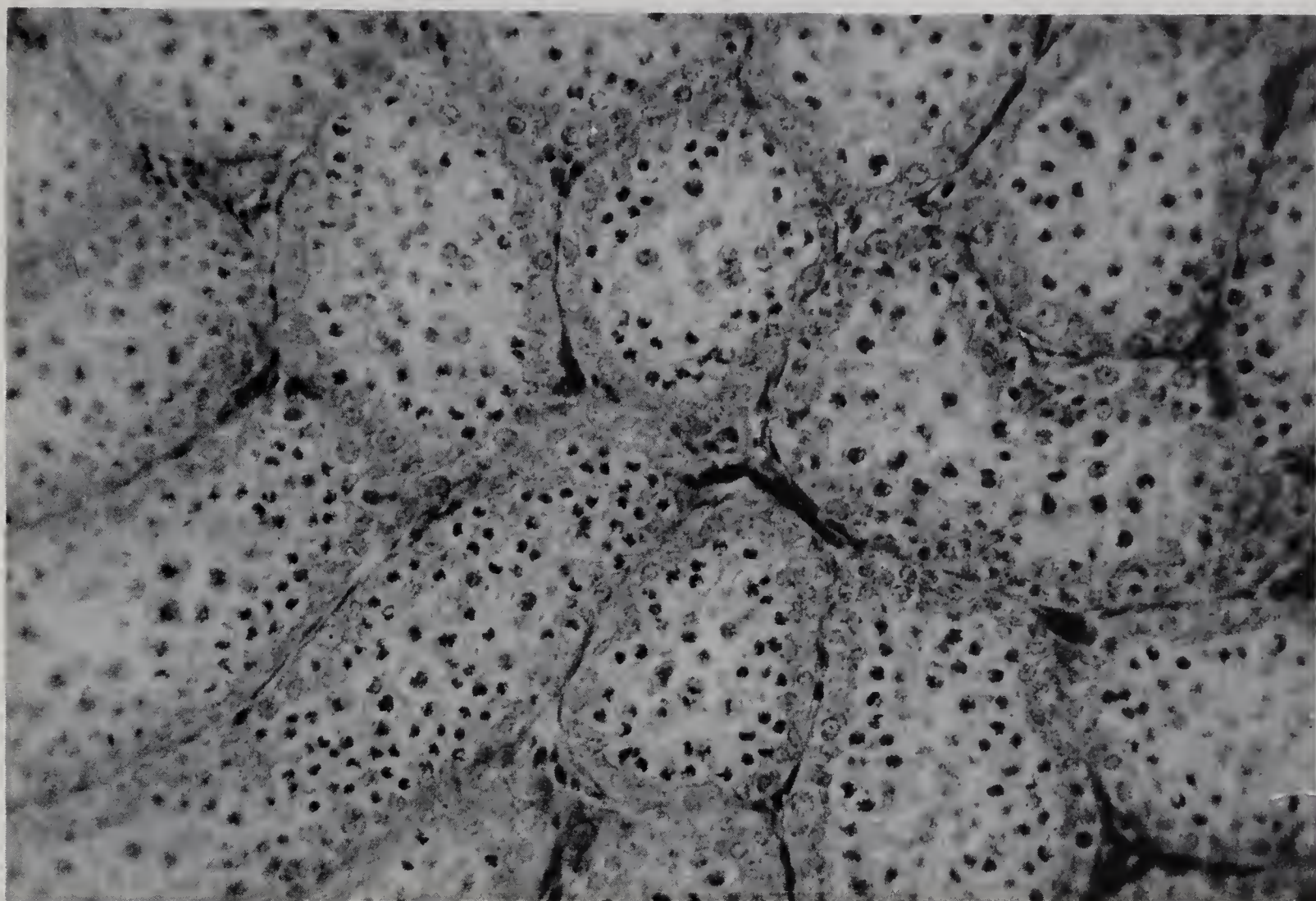
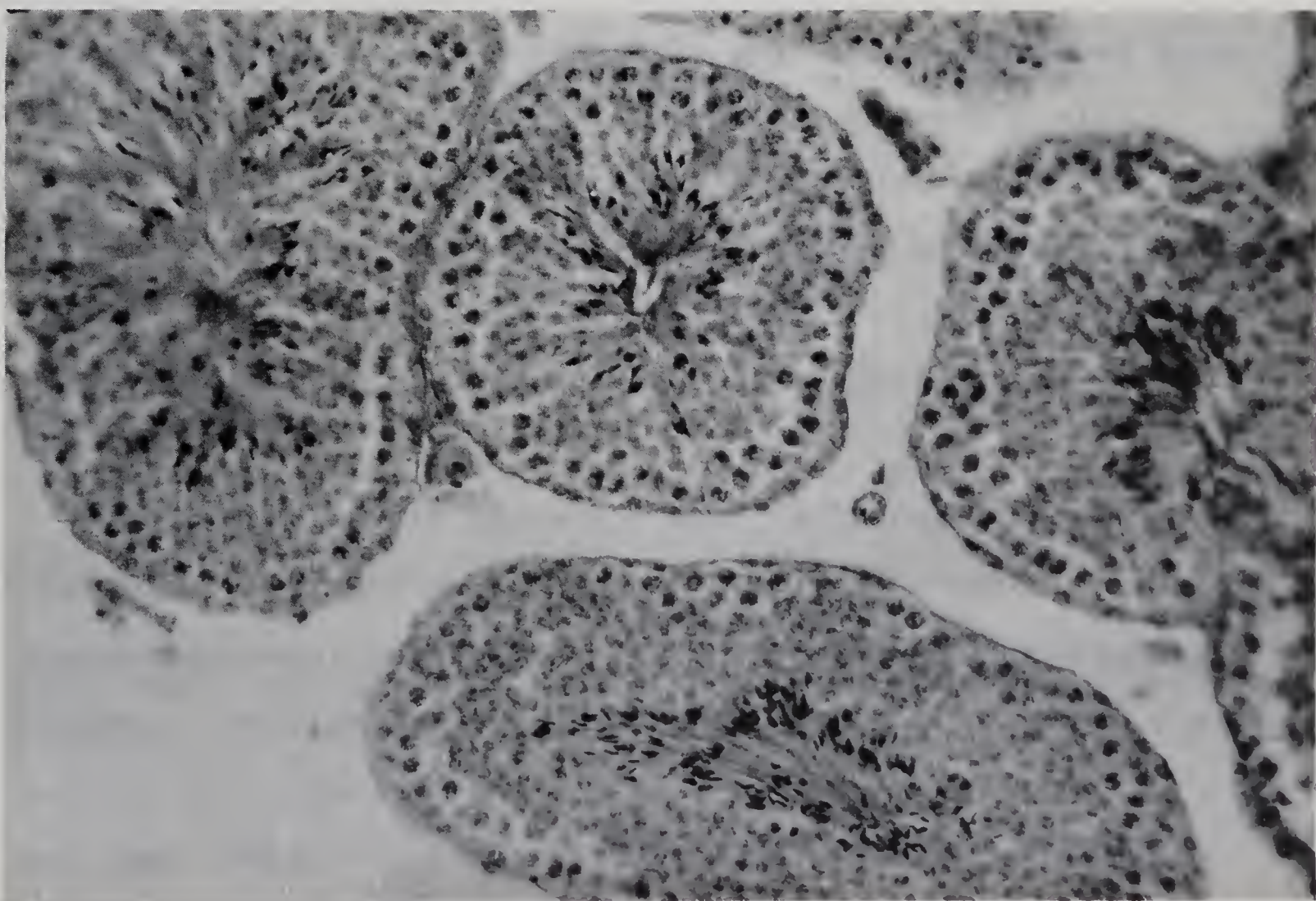
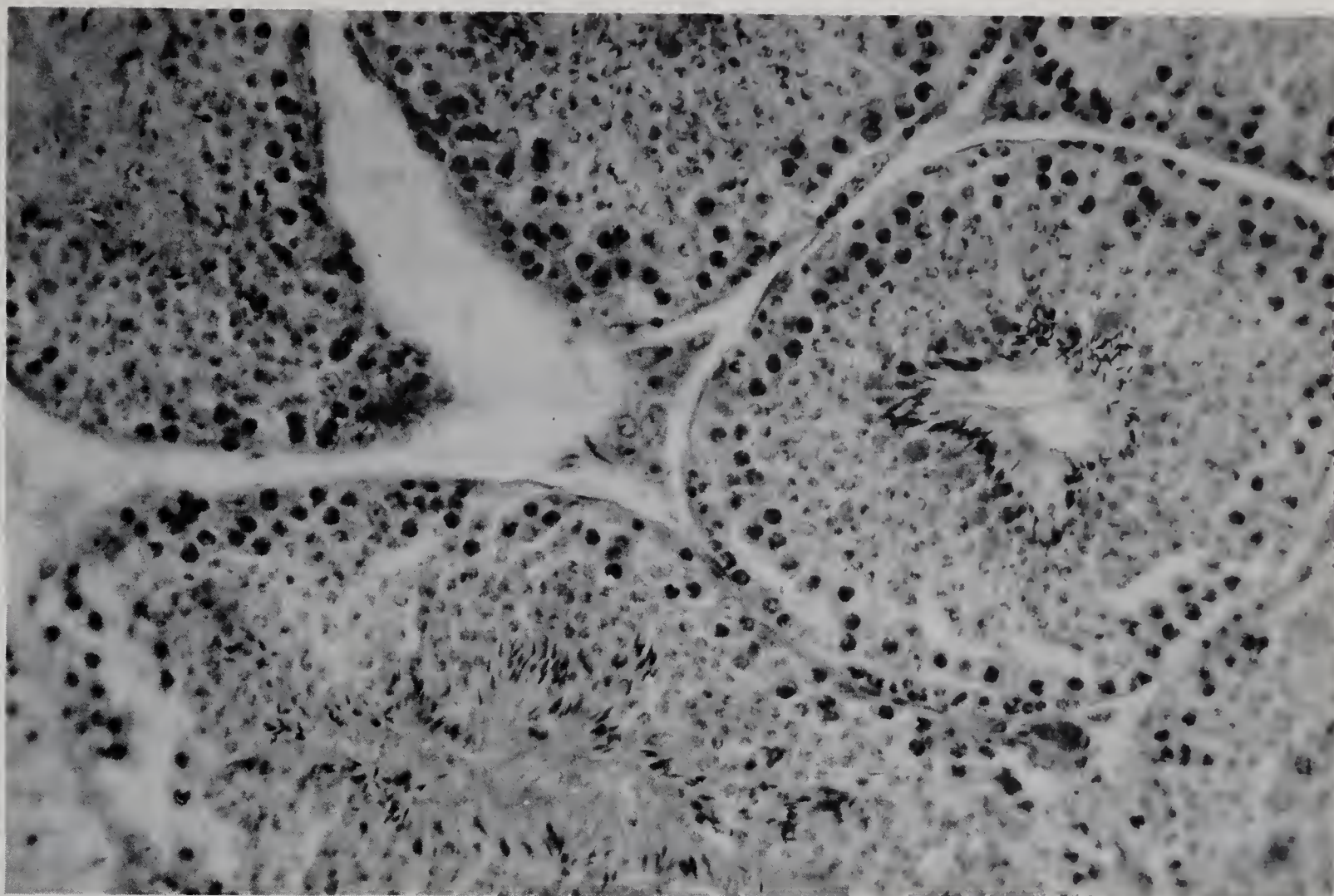


Figure 8. Degree of testicular development:

Stage 3 - obvious quantities of sperm in tubules.

Stage 4 - large quantities of sperm in tubules.



Romer (1962), the same stages are referred to under various names by Maximov and Bloom (1957), DiFiore, (1963) and Zuckermann, (1962).

LABORATORY EXPERIMENTS

Response to Different Wave Lengths

The apparatus designed for this experiment is partially illustrated in Figure 9. It consisted of three chambers, each 4' X 4' X 8', with a 1' X 1' aperture in the ceiling of each to admit light. The chambers were constructed of 1/4" plywood bolted to a metal frame. The joints of the chambers were lined, as an added precaution, with black cloth tape. A door measuring 3-1/2' X 4' was situated on the front of each chamber, and was covered by a flap of black cloth.

The chambers were permanently set up in a darkened basement room, cooled by forced circulation of outdoor air. Lights mounted over each chamber were baffled with black cloth so that no light could travel forward to enter the chambers. It is believed that negligible light was able to enter the chambers except through the aperture provided in the top.

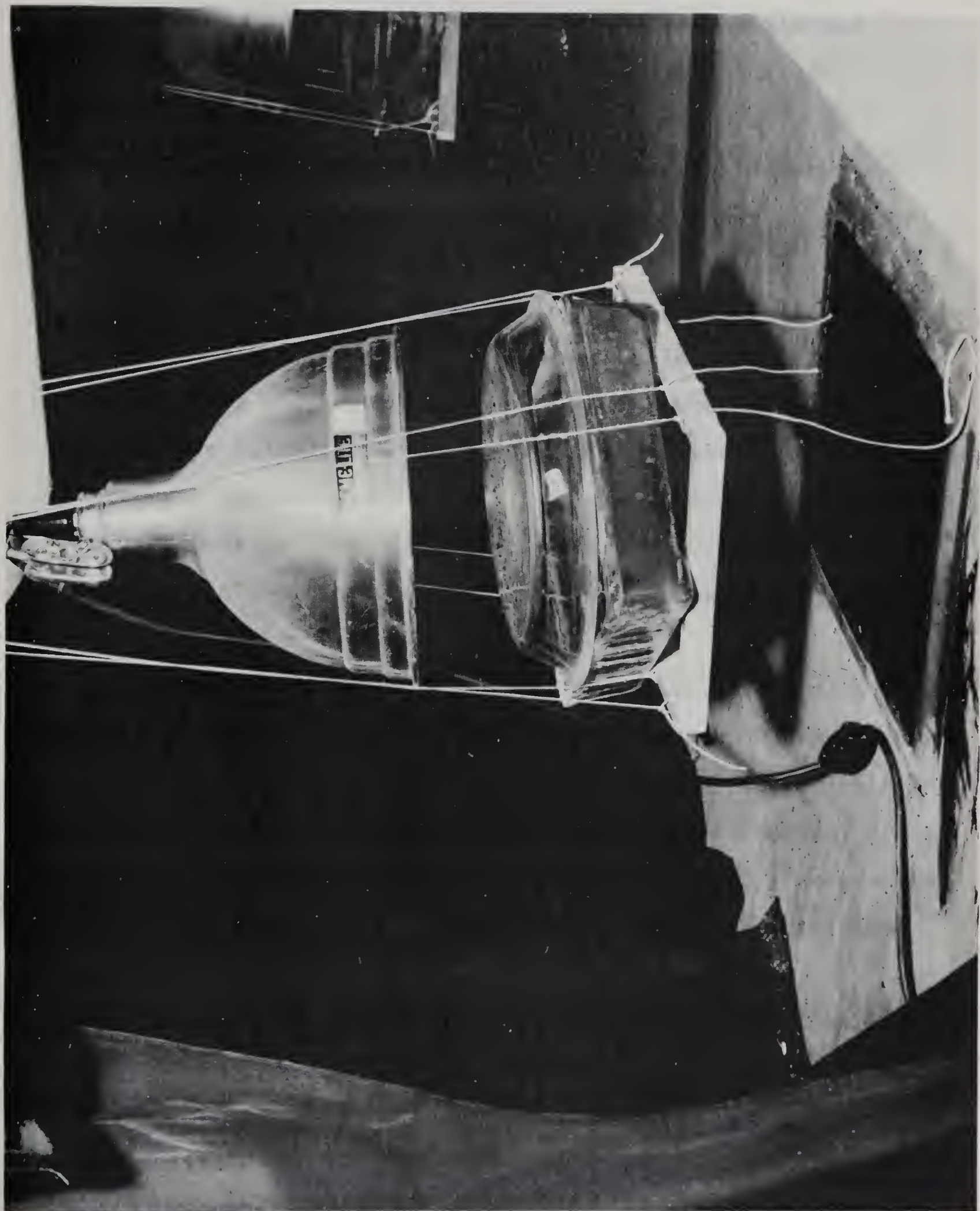
Illumination was via a 150 watt reflector flood lamp (Canadian General Electric Company Limited, Toronto, Ontario) suspended above each chamber. Before entering the chamber, however, the light was required to pass first through a 4 cm bath of 2% copper sulfate, which acted as a heat barrier, and then through a colored filter (CBS filters, available from Carolina Biological Supply Company, Burlington, North Carolina). The filters (red, blue, and neutral density)

Figure 9. Lighting apparatus for wave length experiment.

Top to bottom: reflector containing 150-watt
reflector flood bulb.

2% copper sulfate solution in
pyrex container.

filter, mounted over opening
in roof of chamber.



were of known characteristics such that, when used in conjunction with the copper sulfate bath, light of limited spectral composition and equal energy was transmitted. (Spectral transmittance is shown in Appendix 2). Thus animals in each chamber received light of equal energy and with a minimum of heat, but with different spectral quality in each of the three chambers.

The animals were housed in individual metal cages with a wire mesh top, so situated that each animal could receive the overhead light but could not see the other animals. The cages were placed directly below the light-admitting roof aperture, approximately 5 feet from the actual light source. To guard against the possibility of any unevenness in illumination within the chambers, the cages were rotated each time the animals were checked.

The light flooding chamber #1 was white, since only a neutral density filter was used here. Chamber #2 was illuminated with blue light, and #3 with red light. All animals received 16 hours of illumination daily. The intensity of the light in all chambers was lower than that normally encountered in nature. Laboratory pellet food and water were provided ad lib.

The chambers were filled to capacity, twelve animals in each, at the beginning of the experiment, but initial mortality cut this number to nine in chambers #1 and #3 and eight in #2. This left sixteen females in the experiment, which was all that could be conveniently handled when taking daily vaginal smears.

Animals were examined at three day intervals at first until signs of development began to appear, at which time daily examinations were undertaken. Males could be judged only by descent of the testes into the scrotum, which gives only a crude indication of the developmental stage and is rather difficult to judge accurately in living animals. Consequently, it was decided to sacrifice males periodically so as to obtain a more accurate picture of development.

Females were examined daily to see if the vaginal orifice had become perforate. During the winter months when the animals are sexually inactive, an epithelial membrane is present, leaving no indication of indentation at all (Rowlands and Bramble, 1936). (This is easily distinguished from the vaginal plug of mucus and cornified epithelium found in pregnant animals). The membrane of the developing female becomes perforate spontaneously as the gonads develop. After this event occurs, vaginal smears may be taken to determine when the animal begins to show regular estrous cycles.

In this study, date of perforation was recorded, and, following this, vaginal smears were taken by injecting mammalian saline into the vagina with a pipette and then withdrawing the fluid for microscopic examination. The presence of large masses of cornified epithelial cells was taken to indicate that the animal was in or near estrus.

Near the first of April, the vagina of most of the animals in the white and blue chambers became filled with a so-called "copulatory plug" of mucus and epithelial cells. In females that have not mated, this type of plugging indicates

that a stage called "pseudo-pregnancy" has begun. This often occurs after the animals have undergone several estrous cycles and before they become receptive to males (Rowlands and Bramble, 1936). At this sign, the experiment was ended and all but one female in each test and all of the remaining males were sacrificed. The remaining three animals were retained for 10 days more before being autopsied.

Effect of Light While Under Refrigeration

As previously acknowledged, facilities to maintain winter temperatures were not available, and hence attention was focused on differences induced in spring-caught animals by several wave lengths. However, one small experiment was attempted in a refrigerating unit. In this test, two males and a female were subjected to 16 hours of light per day (using a 40-watt incandescent light bulb), at 4 C. In another group, two males and a female were exposed to 1 hour of light per day and a temperature of 4 C. These animals were otherwise treated the same as those in the wave length test, and were sacrificed and autopsied at the same time as the others. (Note: henceforth, these different photoperiod groups will be referred to in the manner usual for photoperiod literature, i.e., 16L/8C, and 1L/23D.)

Color Preference

To discover whether or not the animals possess any wave length preferences which might cause them to seek out or avoid areas with certain light characteristics, apparatus

was designed to record the frequency with which animals entered a series of feeding chambers flooded by each of several different colors of light.

The apparatus (Fig. 10) consisted of a central nest box 18" square, containing only nesting material and a water bottle. Twelve tunnels leading into separate chambers radiated from this.

In each tunnel there was a false floor, which, when forced down by the weight of the animal, tripped a microswitch. The electrical impulse so created was recorded on an Esterline Angus 20-channel Event Recorder.

Each of the feeding chambers was 6" square and contained 5 pellets of laboratory mouse food. The roof of each chamber was a Kodak gelatin filter (Eastman Kodak Company, Rochester, N.Y., U.S.A.) of known transmitting properties (Appendix 1). The clear glass, the neutral density, the mottled clear, and the black chambers presumably admitted either all wave lengths or none, whereas each of the others permitted a fairly narrow, essentially monochromatic band of light to enter. The filters were mounted in glass to protect them from the mice.

<u>FILTER</u>	<u>DOMINANT WAVE LENGTH</u>	<u>KODAK FILTER NO.</u>
1. clear glass	entire spectrum	
2. green	538 A	74
3. violet	approx. 410	36 + 38
4. red	648 A	70
5. mottled clear glass	entire spectrum	
6. blue-green	480 A	45a

Figure 10. Color preference apparatus.

- A - flood light (in reflector).
- B - central nesting chamber.
- C - water bottle.
- D - peripheral feeding chamber.
- E - filter (comprising roof of feeding chamber).
- F - microswitch arm, with wires connected to
false floor in entrance to feeding chamber.



<u>FILTER</u>	<u>DOMINANT WAVE LENGTH</u>	<u>KODAK FILTER NO.</u>
7. black	nil	
8. neutral density	entire spectrum	96
9. orange	605	72b
10. blue	457.7	50
11. infra red	approx. 1030	87b
12. yellow	576	73

The chambers were illuminated by a Sylvania blue photo-flood of color temperature 5500 K.

After an animal had passed through the test (each animal was retained for about 50 hours in the apparatus), the equipment was thoroughly cleaned and checked: the paper covering the floor was changed, the food replenished, water bottle filled, the chambers deodorized with ordinary household spray deodorant to prevent clues due to urination by the previous occupant, and the filters were rotated about the central chamber. Following this procedure, a new animal was introduced.

Twenty Clethrionomys gapperi were allowed to spend time in the apparatus. The graphs were later analyzed by counting the number of entries into each chamber. As a safeguard against the possibility of an animal hovering on the verge of entry and so tripping the switch several times while making only one entry, the more conservative measure of "number of 10-minute intervals containing entries" was also recorded. Both of these were then totaled, and the percentage of total entries attributed to each chamber was recorded.

This experiment was designed only to give an indication

of any trends in color preference. It cannot be stated that the results conclusively indicate such a preference. However, facilities were entirely lacking at this University to determine the amount of light energy which was actually flooding each chamber. That is, one may be sure of what colors are reaching the animals, in each chamber, but not of the energy level reaching them.

RESULTS

SUBNIVEAN LIGHT

Tracings from the three subnivean meters described in the previous section are illustrated in Figure 11. The arbitrary units on this graph were obtained by a summation of light values at hourly intervals throughout each day. For comparative purposes, this indicates quite clearly the changes in intensity which occurred, despite the complicating factor of having to also consider photoperiod in the same unit.

This figure demonstrates that, during the winter months, there is exceedingly little visible light present in the subnivean environment and that the occupants are therefore existing in conditions approaching total darkness. It should be noted that in the habitat most frequented by C. gapperi, represented by station #2 (poplar forest), the decrease in light was especially dramatic. Light levels were too low for my selenium cell to detect, and remained so from 13 January to 20 March.

Station #1:

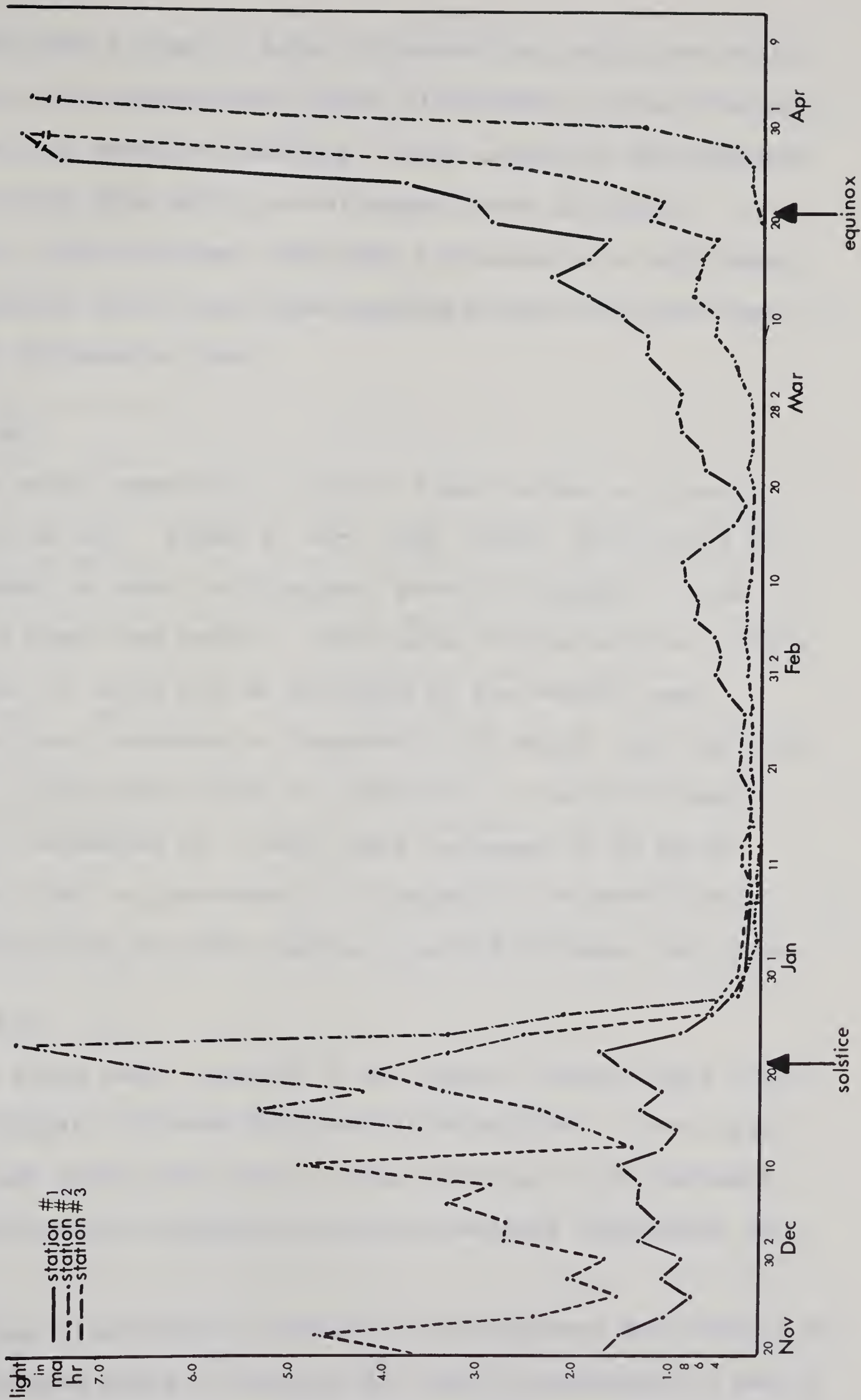
Light reaching the meter located in the open clearing station is seen to have remained at a fairly constant level up until 24 December. This meter does not reflect the progressive decrease in illumination one would expect to find as the shortest day is approached. Rather, a marked decline occurs after 21 December, and light remains at a low level (< 0.20 units) until the end of January.

Figure 11. Subnivean light levels at three stations throughout the winter of 1965-1966.

Station #1 - open clearing.

Station #2 - poplar forest.

Station #3 - spruce forest.



Note that a rise in total illumination, which one would expect to occur immediately after 21 December, occurs during the first two weeks in February. Only a drop in mid-February prevents this from being a continuous trend through to 14 March. Shortly after that date increases of a high magnitude occurred daily until the recorders had to be shut down for fear of damaging them.

Station #2:

The meter operating in poplar forest shows no signs of ambiguity at all. Light at very high levels (9.00 units on 21 December) is seen to disappear from the records in the period of about one week to leave this station with so little light that it could not be detected by the meters used.

The first increase is observed on 22 March, and the slow rise in illumination which is indicated in the 22-25 March period is succeeded by a very sharp increase on 30 March. In effect then, an increase in illumination of more than a thousandfold was recorded during a period of about ten days.

Station #3:

The light meter located in the spruce forest shows light levels similar to those indicated in station #2. Once again, rather high levels give way to near darkness on 25 December, to be followed by constantly similar readings throughout the winter.

Spring illumination increases are indicated for station #3 some two weeks ahead of station #2, and the subsequent rise is much more gradual than that at the previous station. Once

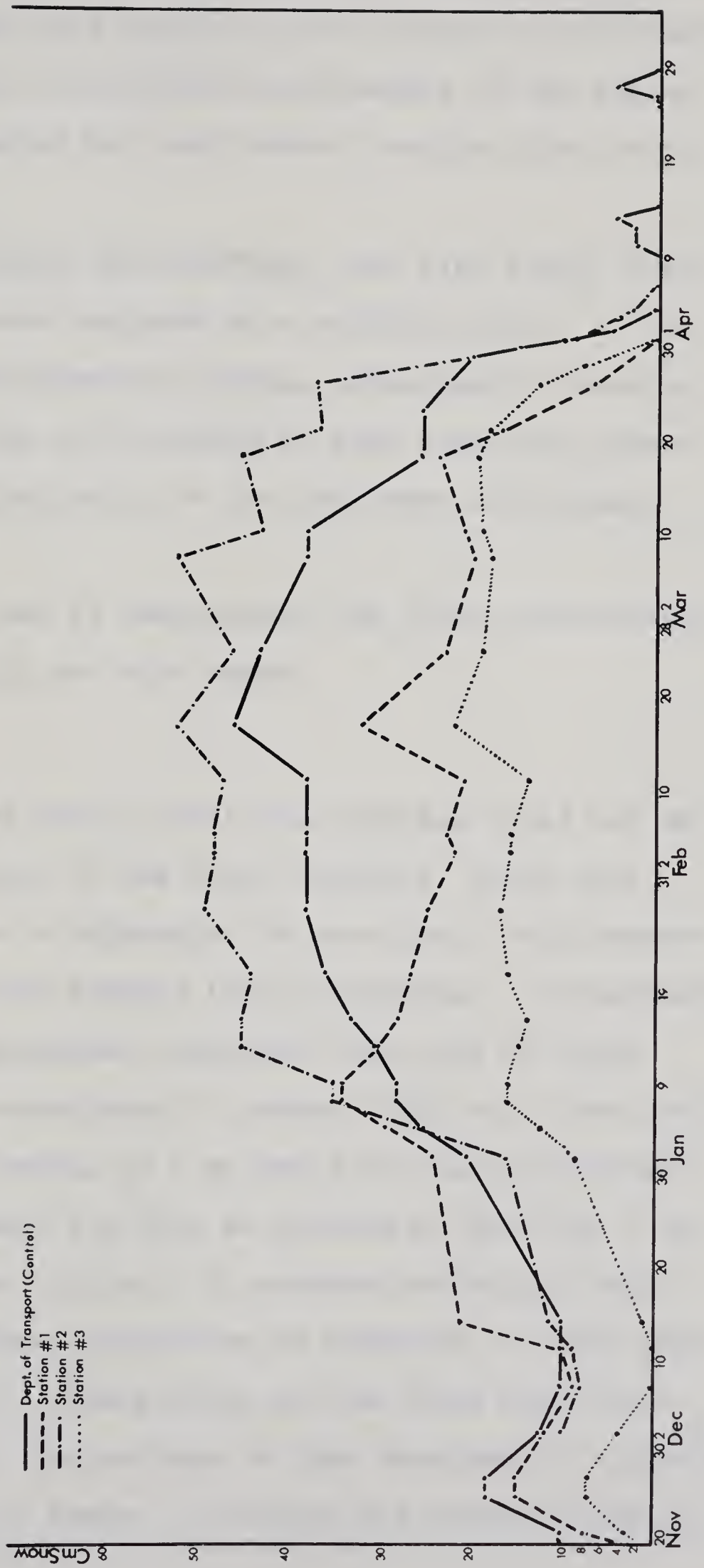
again though, a considerable increase in illumination is indicated over a fairly short period, although neither the magnitude of the change nor the shortness of the transition period are nearly as dramatic as those at station #2. Commencing its rise on 4 March, station #3 indicates an increase of 120-fold by 31 March. This is a very conservative estimate of the actual increase, however.

Even the thousand-fold increase shown at station #2 is conservative, for no indication of actual intensity can be perceived once the galvanometer has reached its maximum deflection. All three recorders were giving maximal readings for some time before the study was ended (first maximal reading on 26 March for station #1, 2 April for station #2, and 27 March for station #3). Therefore, after these dates, all calculations are of minimum illumination for that date. The reason the readings of station #2 are about ten times as high as the other two is that this recorder was capable of reading to 10 ma, the others only to 1 ma. Thus one may presume that all stations actually experienced a rise in total illumination at least as great as the 1000% increase shown at station #2.

CORRELATION OF LIGHT INTENSITY AND SNOW DEPTH

Figure 12 illustrates the rates of snow accumulation at the three subnivean light stations and at the Department of Transport control plot. Inclusion of the official Department of Transport snow depths illustrates clearly the change in snow depth which occurs under normal field conditions: snow from the open clearing (station #1) is being blown into and

Figure 12. Snow depths at three subnivean light stations and at a control plot operated by the Department of Transport, Meteorological Bureau, at the Edmonton International Airport.



retained by the poplar forest (station #2). Presumably both stations received snow fall similar to the control, but alteration by wind has made the subnivean environment of the poplar forest a better insulated but much darker one than that found in the open field.

Deep snow, resulting from drifting, was also found in the trapping area, which was bordered by a stubble field. It is clear, then, that environmental changes subsequent to snowfall have a distinct bearing on the depth of snow cover and consequently on the characteristics of the subnivean environment in any given area.

Figures 13, 14, and 15 demonstrate the close relationship between light intensity and snow depth.

Station #1:

The reader should realize that the recorder could not be allowed to operate prior to the first snowfall, since this would have resulted in a deflection of more than 1 milliamper, and could therefore have damaged the galvanometer. Consequently, the starting date 20 November represents the date at which sufficient snow had accumulated to reduce light to a level such that a deflection in excess of 1 ma would not be encountered. The snow depth necessary for this at station #1 was only 3 cm. This is not surprising, since it is surface reflection which accounts for the greatest proportion of decrease in light penetration (Geiger, 1950). The portion of the light which does succeed in penetrating the surface is then absorbed to a greater degree as it penetrates deeper, following the formula cited in

Figure 13. Light levels and snow depths at Station #1.

STATION #1

— Snow
- - - Light

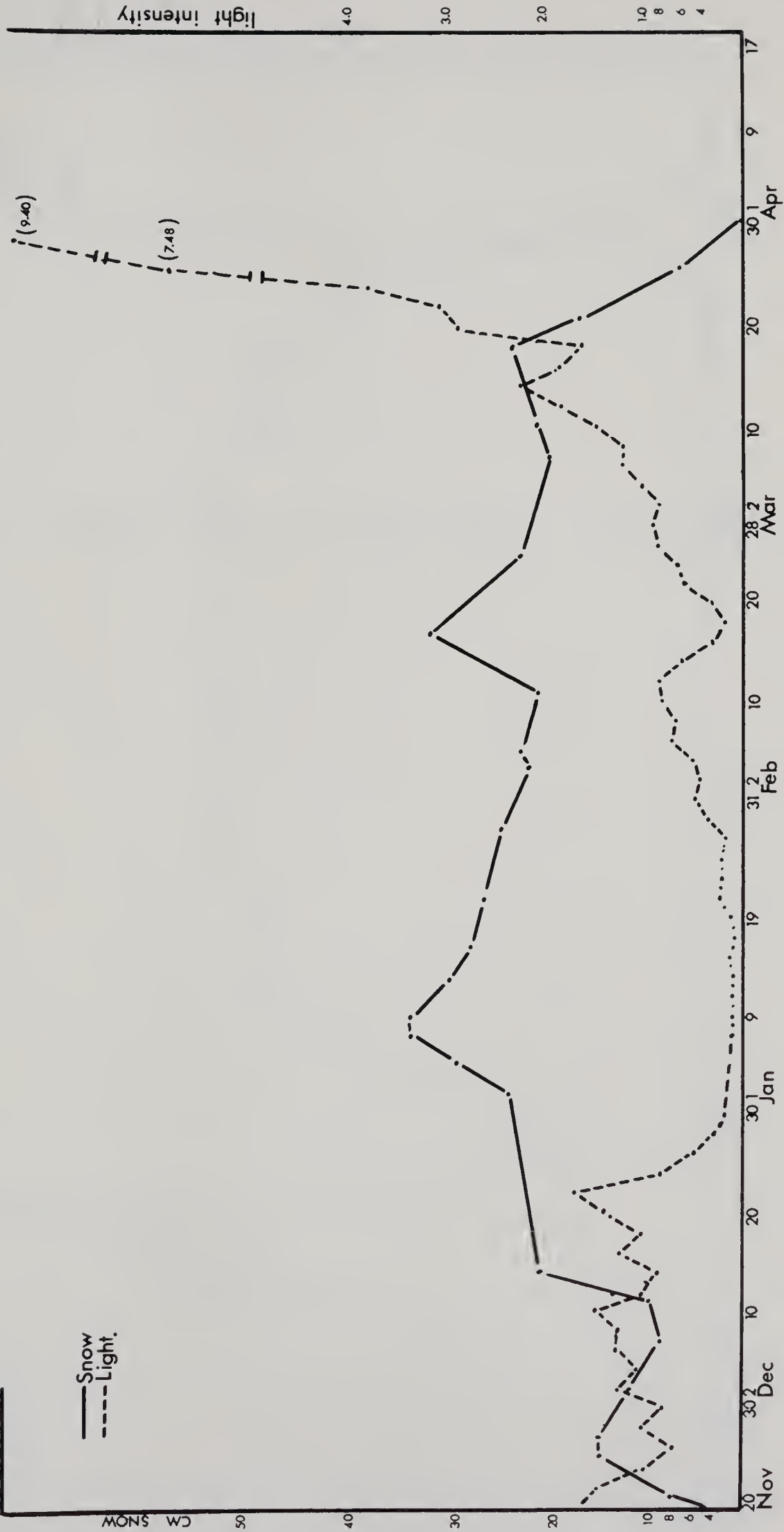


Figure 14. Light levels and snow depths at Station #2.

STATION # 2

— Snow
--- Light

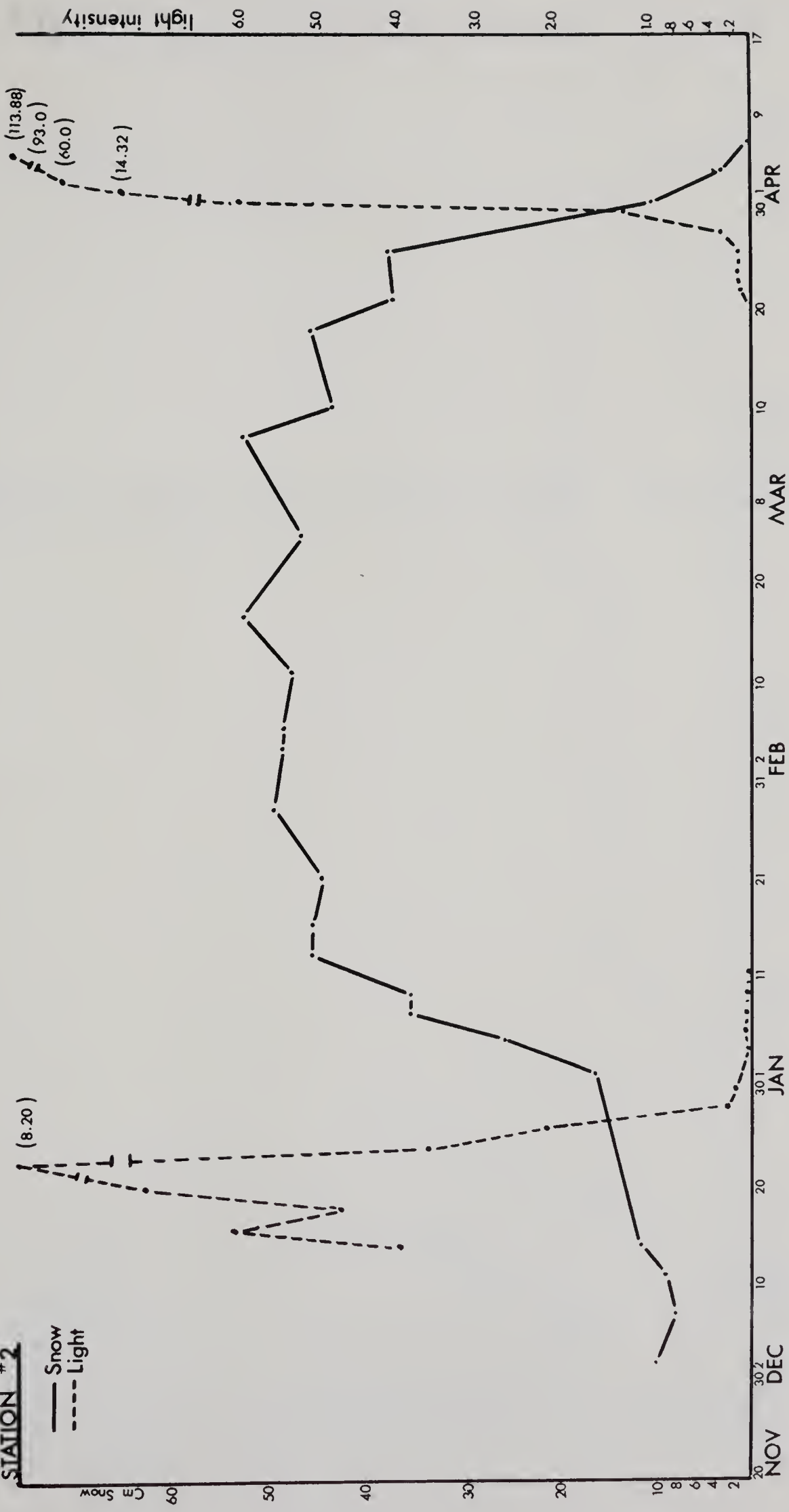
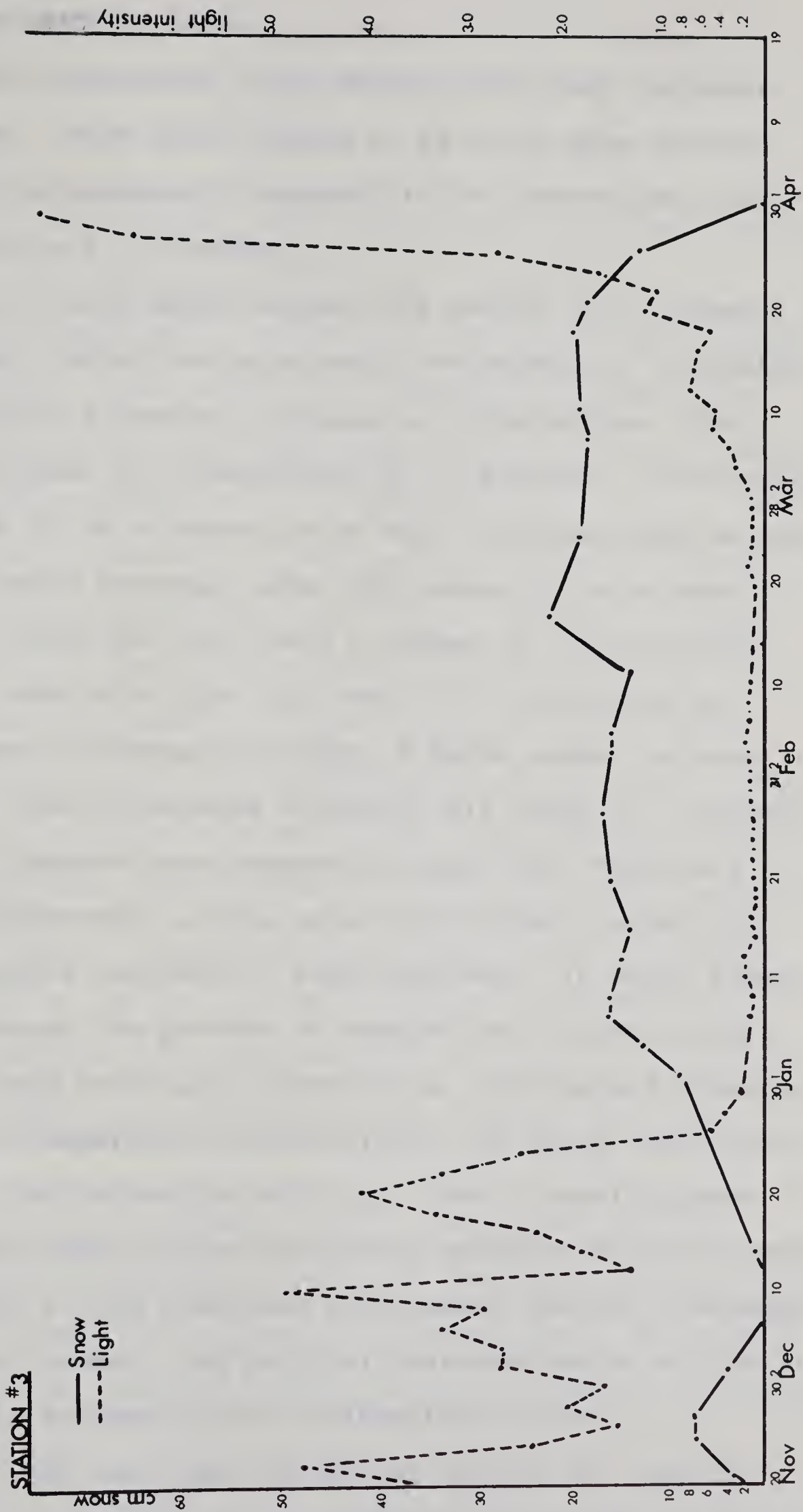


Figure 15. Light levels and snow depths at Station #3.



the discussion section below.

Figure 13 illustrates light decrease and snow increase for station #1. Note that a depth of 24 cm of snow in the early winter was apparently responsible for decreasing light values to near zero (1 January).

Decrease in snow depth between the period of 10 January and 12 February, which was apparently due primarily to blowing, is accompanied by a gradual increase in illumination. The fact that the level of illumination on 12 February (0.80 units), achieved under 21 cm of snow, is as high as those found in late November and early December under only about 15 cm of snow suggests that there has also been a change in the structure of the snow. Note also that the level of illumination is increasing from 20 February through 14 March under the same depth, 24 cm, that eliminated virtually all light on 1 January. Both of these observations suggest strongly that there are qualitative differences in the snow which alter its ability to reflect visible radiation. More precisely, it would appear that it is through the process of weathering (losing crystal dendrites through mechanical disturbance, melting and freezing in response to temperature fluctuations, and so on) that snow loses some of its reflecting ability. Thus it would appear that one cannot judge subjectively what quantity of light energy will be present in the subnivean environment through knowledge of depth alone; rather, the physical characteristics of the snow cover must be taken into consideration as well.

The fact that the light reflecting ability is lost as winter progresses suggests the possibility of a light increase

even under depths of snow which seem adequate to block all light.

Station #2:

Figure 14 demonstrates very clearly the reciprocal arrangement between snow depth and penetrating illumination. It should be remembered that it is in this habitat that C. gapperi was most commonly found (along with Peromyscus maniculatus) and that depths of the magnitude indicated are the rule rather than the exception under natural circumstances.

Again, as at station #1, snow depths of 20-25 cm appear to have removed all detectable light by 11 January. However, it is important to observe that once again, as at station #1, light increases are observed in the spring at depths great enough to have obstructed all illumination in the fall. This may be partly a function of atmospheric light intensity being greater in the spring than in the fall, but, as noted earlier, it is likely also a function of snow metamorphosis occurring at the approach of spring. In this particular example, 25 cm of snow blocked all light detectable by the meter in the fall, whereas some light was recorded at a snow depth of 36 cm in the spring.

Station #2 is outstanding for the very short period indicated between apparent darkness and extreme brightness in spring, which Figure 14 demonstrates to be closely correlated with the similarly dramatic disappearance of snow in the spring.

Station #3:

Station #3 records confirm the recurrence of the phenomenon of light increase under previously light-obscuring snow depths. It would seem that under spring snow conditions, light increases can occur even at a slightly greater depth (18-20 cm) than had previously been sufficient to maintain a consistently low level of illumination during the winter (approx. 16 cm). This again emphasizes the importance of qualitative as well as quantitative effects of snow on light penetration.

It should be noted that the light-shielding effect of snow is supplemented by the shade of the spruce trees (Atkins and Poole, 1937b). But while these trees shade the forest floor, they are also responsible for the low depth of snow on the ground. Falling snow is interrupted by the evergreens and remains on their branches as a form of snow called "qali" by Pruitt (1957). How the addition of snow to the branches affects the intensity and spectral composition of the light penetrating the forest canopy is open to speculation.

SUBNIVEAN PHOTOPERIOD

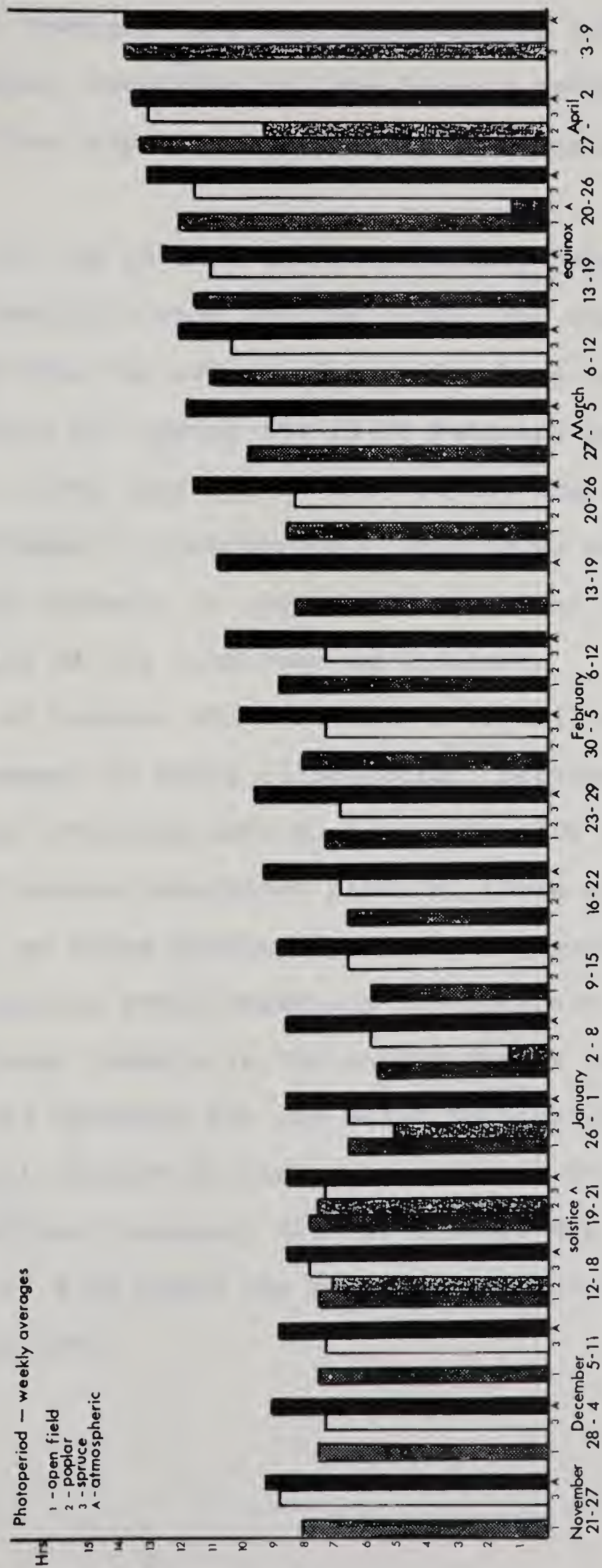
While being generally less dramatic than changes in total light energy in the subnivean environment, photoperiod is also seen to vary inversely with snow depth despite constantly increasing day length from 21 December onwards.

Average photoperiods during weekly intervals throughout the fall, winter, and spring are shown for each of the subnivean stations and for the atmospheric station in Figure 16. It is quickly seen that except in the case of station #2, photoperiod

Figure 16. Weekly average photoperiod at three subnivean and one supranivean light stations.

Photoperiod — weekly averages

- 1 - open field
- 2 - poplar
- 3 - spruce
- A - atmospheric



is not prevented from increasing with the approach of spring. It is also clear, however, that the initiation of increase is considerably delayed, occurring in late January rather than on 21 December. The slope of the increase is accentuated by snow.

Figure 17, 18, and 19 show the relationship between photoperiod and snow depth for each station, again for weekly periods. Stations #1 and #3 show the effect of snow depth quite well. Note that at station #1, during the 13-19 February period in which there was a sharp increase in snow depth, there is a corresponding decrease in photoperiod. This shows again how effective a slight increase in snow depth can be in altering the characteristics of the subnivean environment.

Station #2, of course, shows results every bit as dramatic as it did with respect to total illumination, because total darkness certainly indicates zero photoperiod. How closely the rodents' light-sensing abilities parallel those of the selenium cell is, as noted previously, an open question. The answer to this question would determine how accurate it is to report that subnivean rodents in the poplar forest were forced to experience total darkness for the major portion of the winter.

Photoperiod at station #2 begins to increase during the 20-26 March period and increases from 1.25 hours day length during this week to 9.25 hours the next week and 13.75 hours the week following that.

Figure 17. Snow depths and weekly average photoperiod
at Station #1 during the winter of 1965-1966.

STATION #1



Figure 18. Snow depths and weekly average photoperiod
at Station #2 during the winter of 1965-1966.

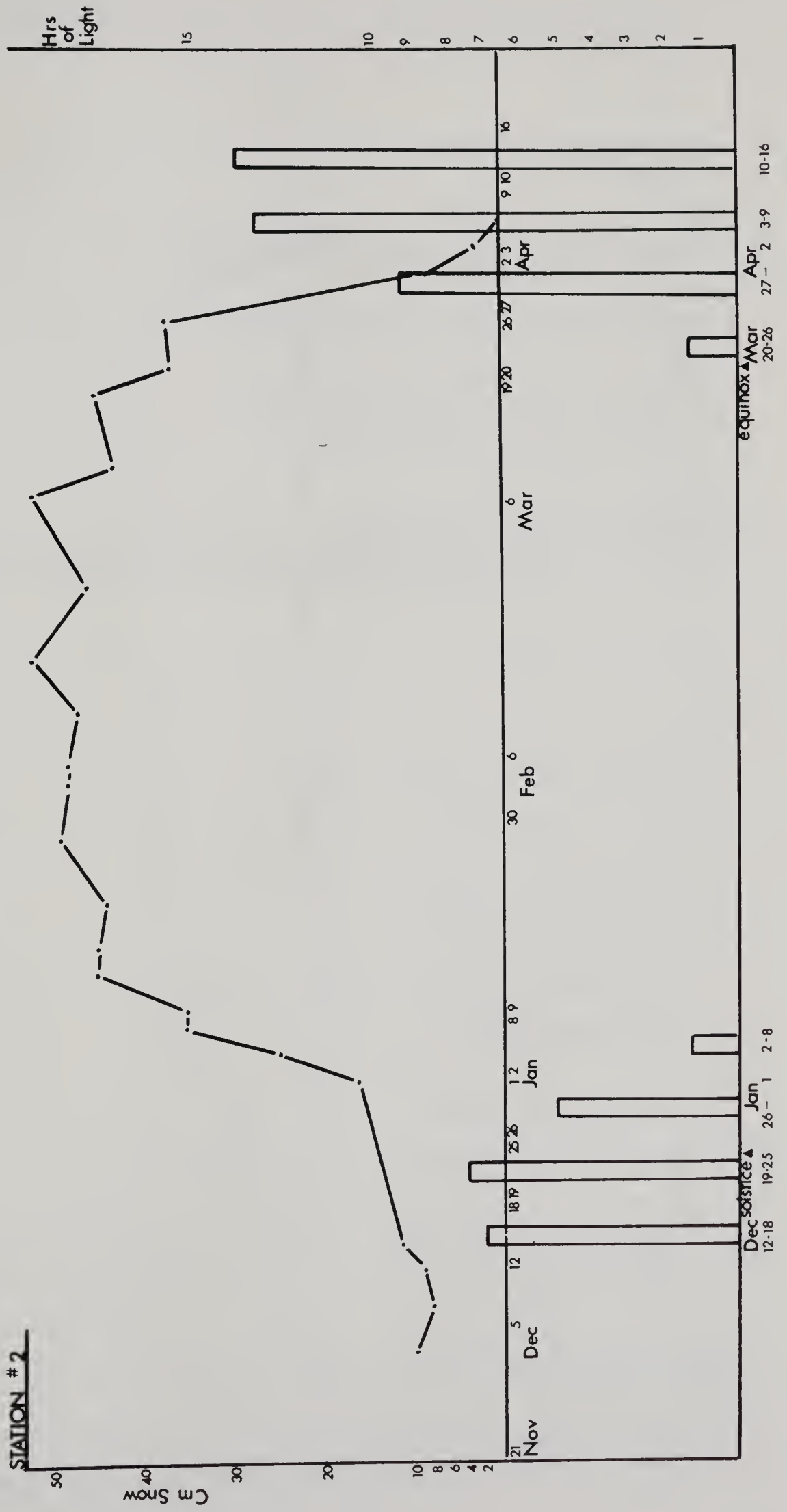
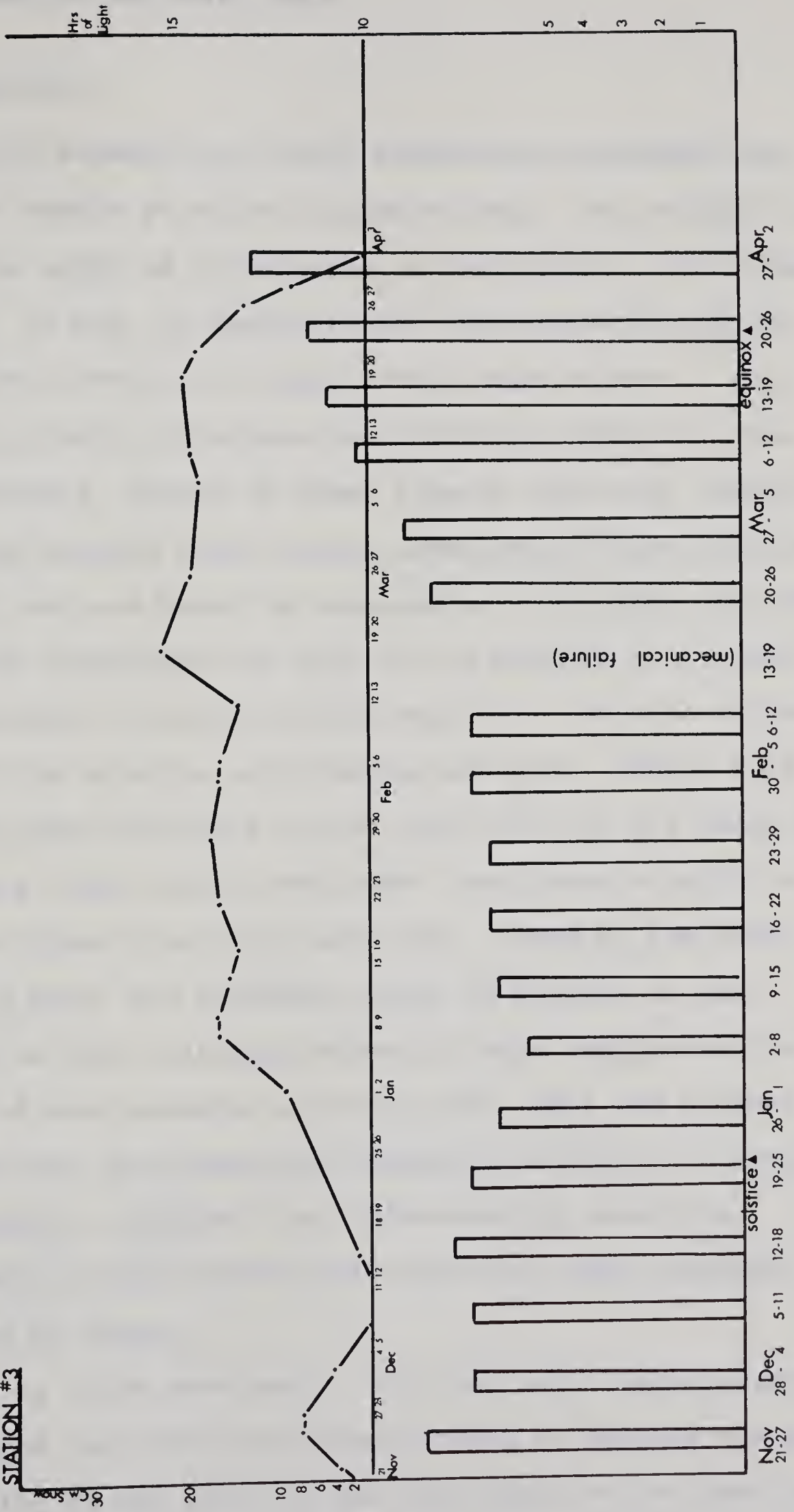


Figure 19. Snow depths and weekly average photoperiod
at Station #3 during the winter of 1965-1966.

STATION #3



COLOR TEMPERATURE AND SNOW DEPTH

Color Temperature

Figure 20 presents all color temperature readings taken and the snow depths at which they were taken. No account is taken in this graph of differences in atmospheric color temperature (which, as Fig. 21 demonstrates, fluctuates during the course of the winter) or of qualitative snow changes. Thus this figure probably minimizes the filtering effect of snow.

Nevertheless, Figure 20 shows clearly the shift towards the long wave lengths which occurs immediately below the surface of the snow and which is enhanced as snow depth increases. This fact has importance not only to the mammals in the subnivean environment (see discussion section), but also to the readings of the selenium cells mentioned above. These cells are slightly more sensitive to red light than is the human eye, and therefore light levels read under considerable depths of snow may be higher than would have been judged by the human eye. At any rate, the essential point to realize is that recognition of this filtering effect by snow complicates our conception of what amounts of perceivable light are present in the subnivean environment and presents problems of converting from the energy output of the differentially sensitive selenium cells to the conventional units of light intensity as perceived by humans.

Since, as noted previously, plotting color temperatures without regard for modifying factors tends to obscure the very close relation of the shift to the red region of the spectrum

Figure 20. Shift in color temperature with increasing snow depth.

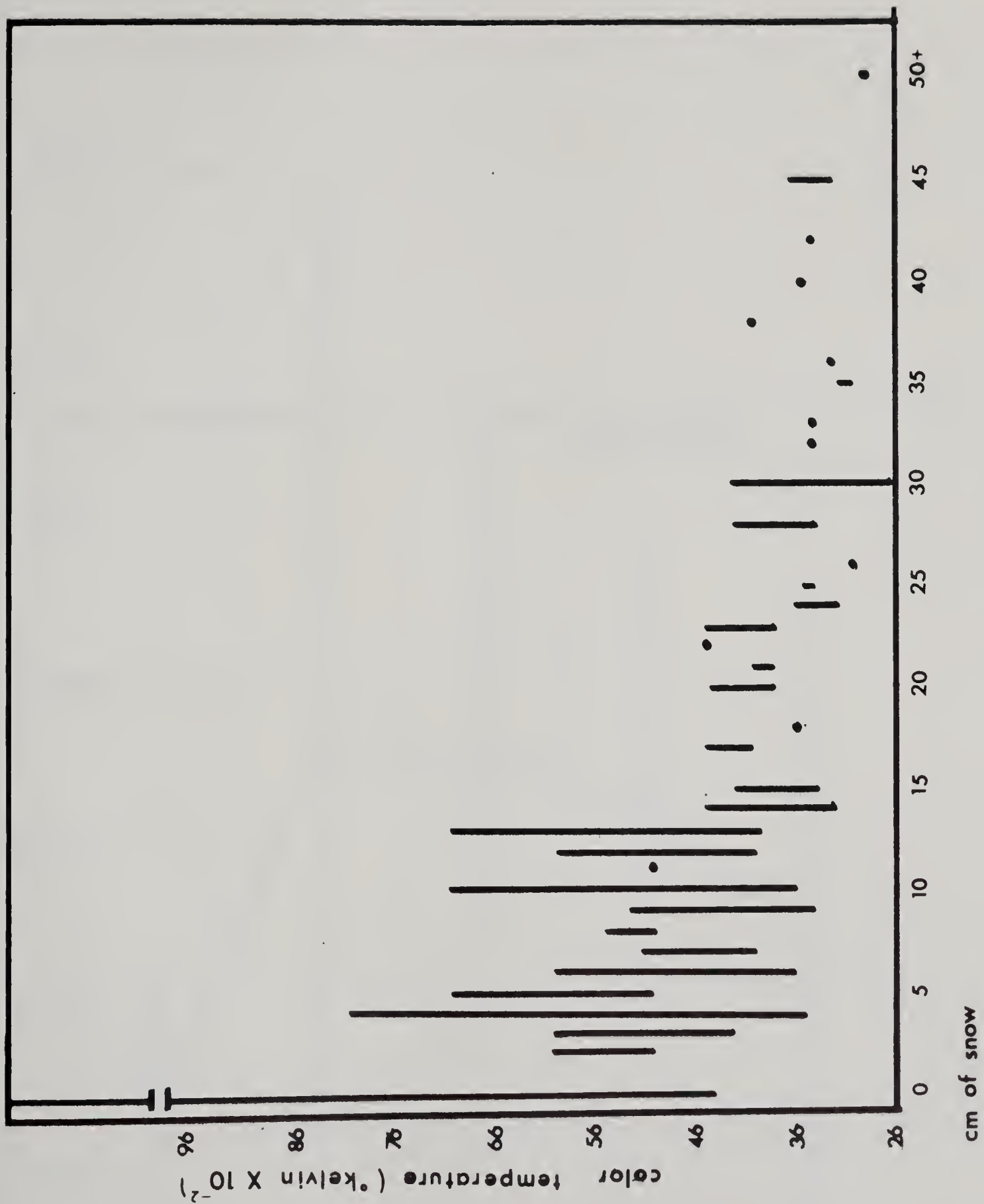
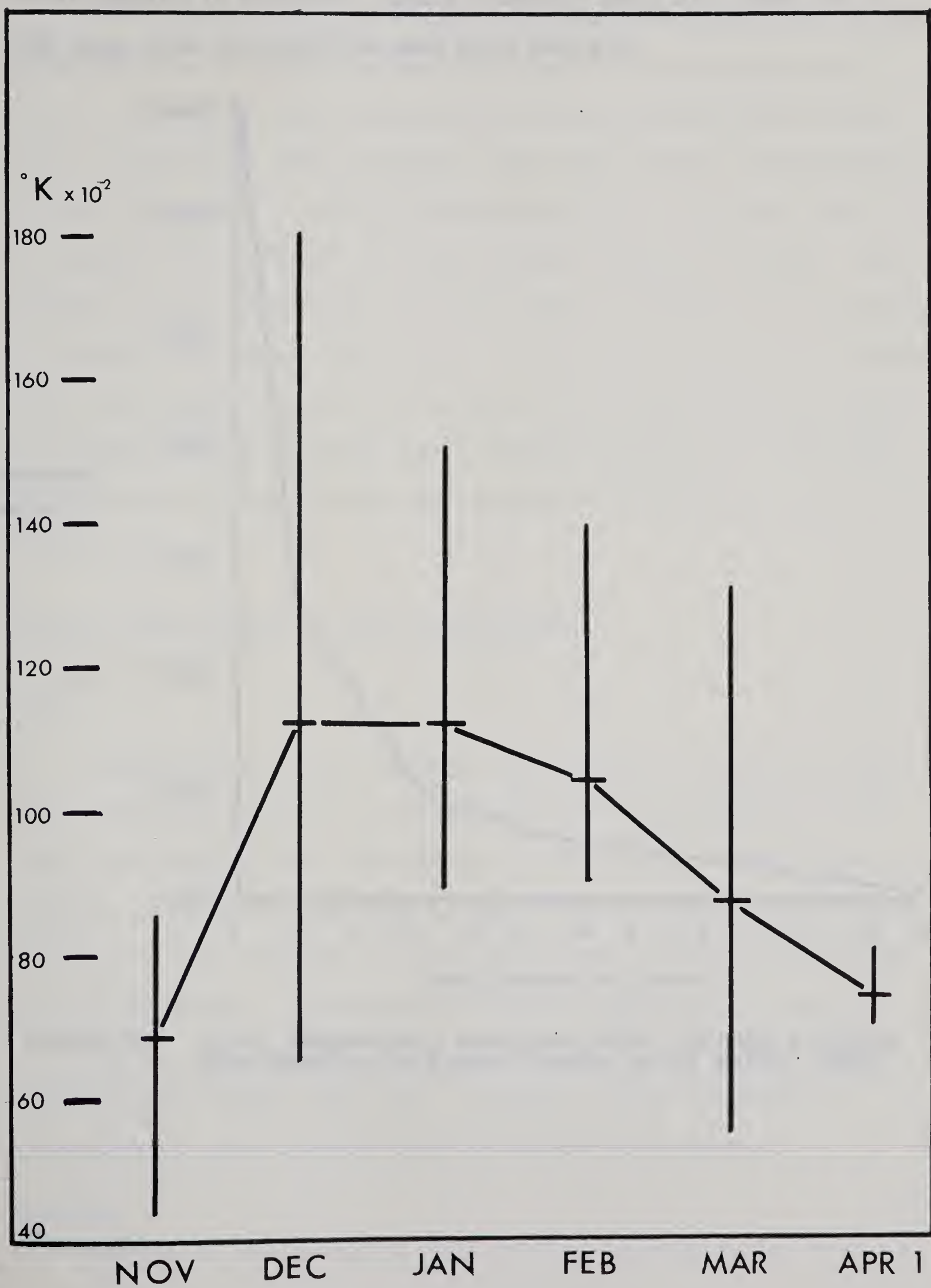


Figure 21. Changes in average monthly atmospheric color temperature.



with increasing snow depth, the following example of this relationship is offered. These readings were all taken at the same time through the same snow profile.

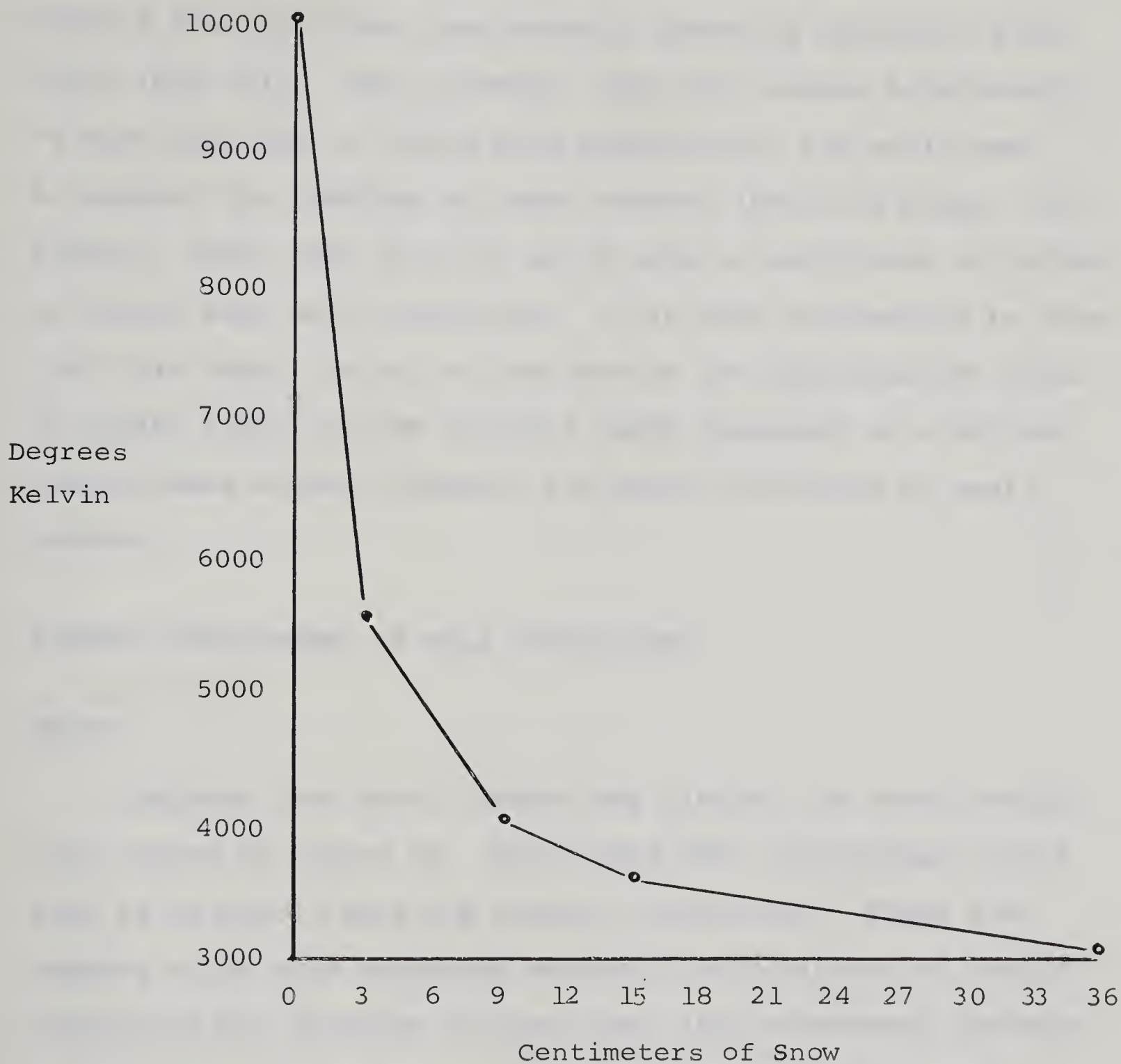


Figure 22. Color temperature readings taken through a single snow profile in poplar forest on 27 March, 1966.

Light Intensities

These data, (taken through snow profiles along with color temperature), do little more than support the observations derived from the three continuously operating subnivean light cells (Fig. 23). They, however, show the inverse relationship of snow and light a little more graphically, and would seem to support the findings of other workers (Nees and Bunge, 1957; Kalatin, 1951) that 10 to 15 cm of snow is sufficient to deflect or absorb most solar radiation. It is also interesting to note that this depth, 15 cm, is the same as the approximation given by Pruitt (1957) as the critical depth necessary to stabilize temperatures at near freezing and permit burrowing by small mammals.

NATURAL DEVELOPMENT IN WILD POPULATIONS

Males

Trapping from March through May yielded the testis weight curve shown by Figure 24. From these data, development would seem to be quite rapid and notably synchronous. There also appears to be some synchrony between the initiation of testis growth and the decrease in snow depth (and consequent increase in illumination), as demonstrated by Figures 25, 26, and 27.

During the month of March, there was also a considerable gain in body weight (Fig. 28). However, this increase is considerably more gradual than is testis development.

Females

Figure 29 demonstrates that females underwent increase as

Figure 23. Shift in light intensity with increasing snow depth (as indicated by a Weston Mark IV light meter).

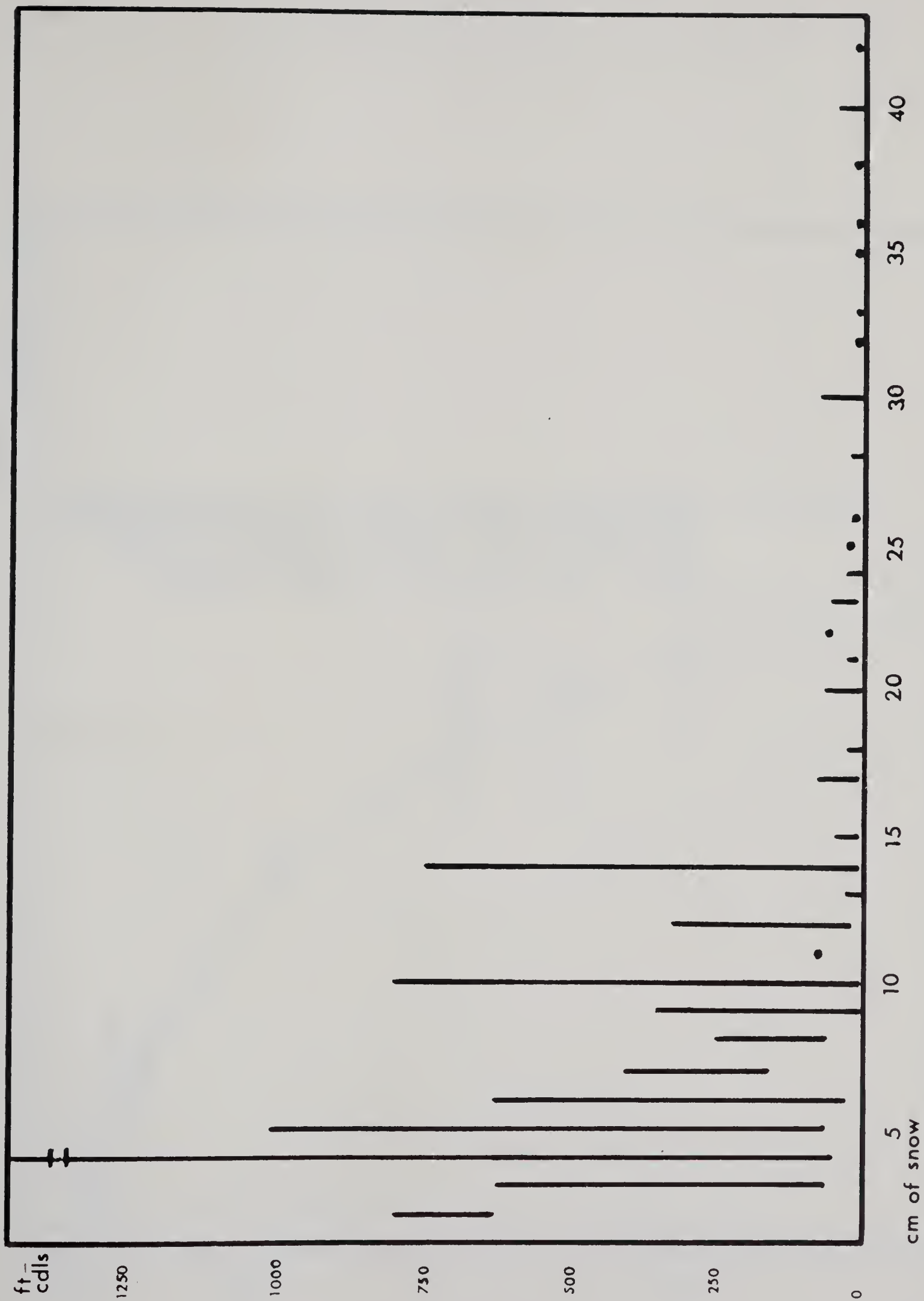


Figure 24. Testicular growth curve for wild population. Horizontal bars represent range in weights of testes from animals captured on that date. Dots represent single animals.

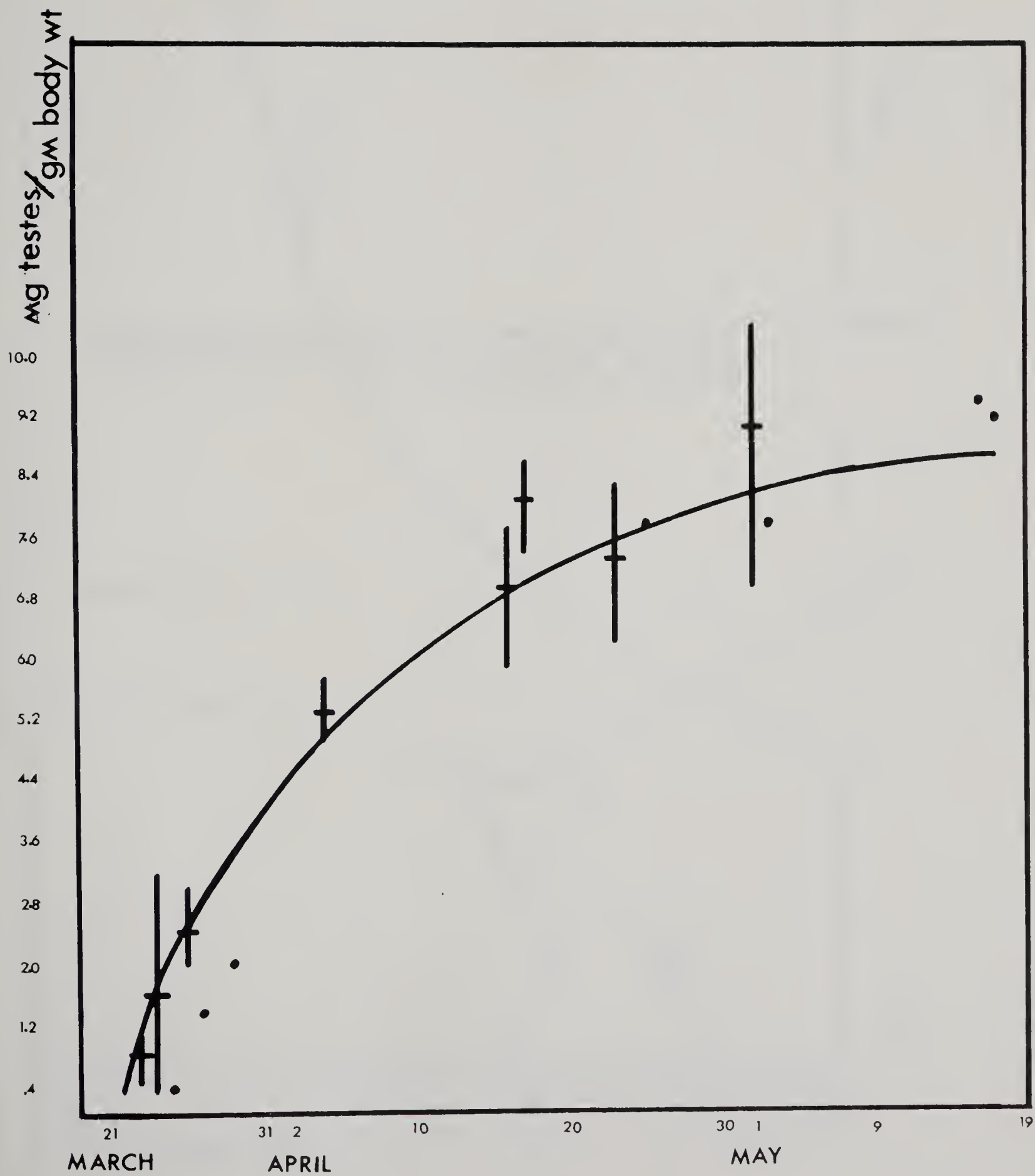


Figure 25. Testicular growth curve of wild population shown in relation to light and snow depth changes at station #1.

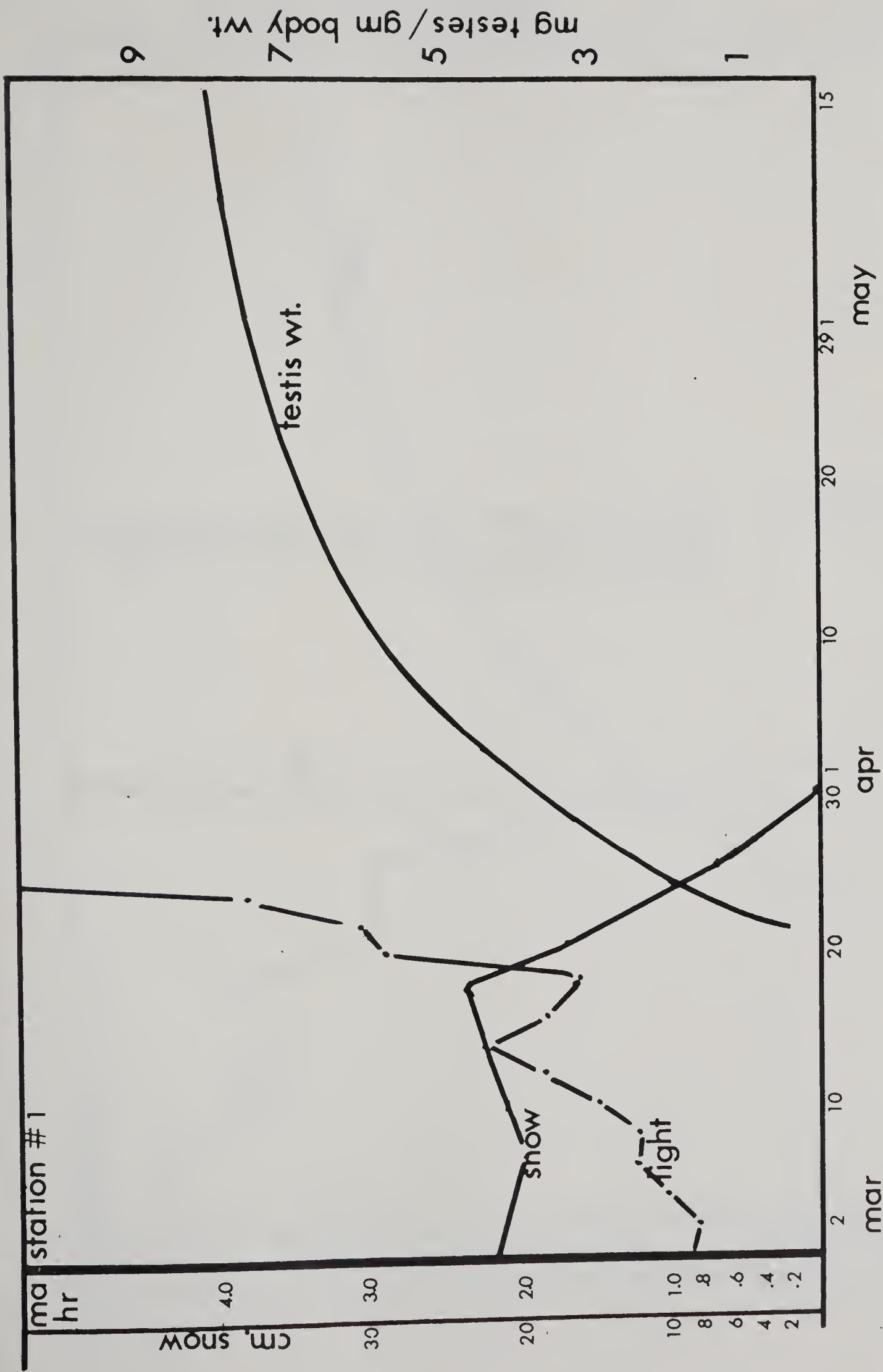


Figure 26. Testicular growth curve of wild population shown in relation to light and snow depth changes at station #2.

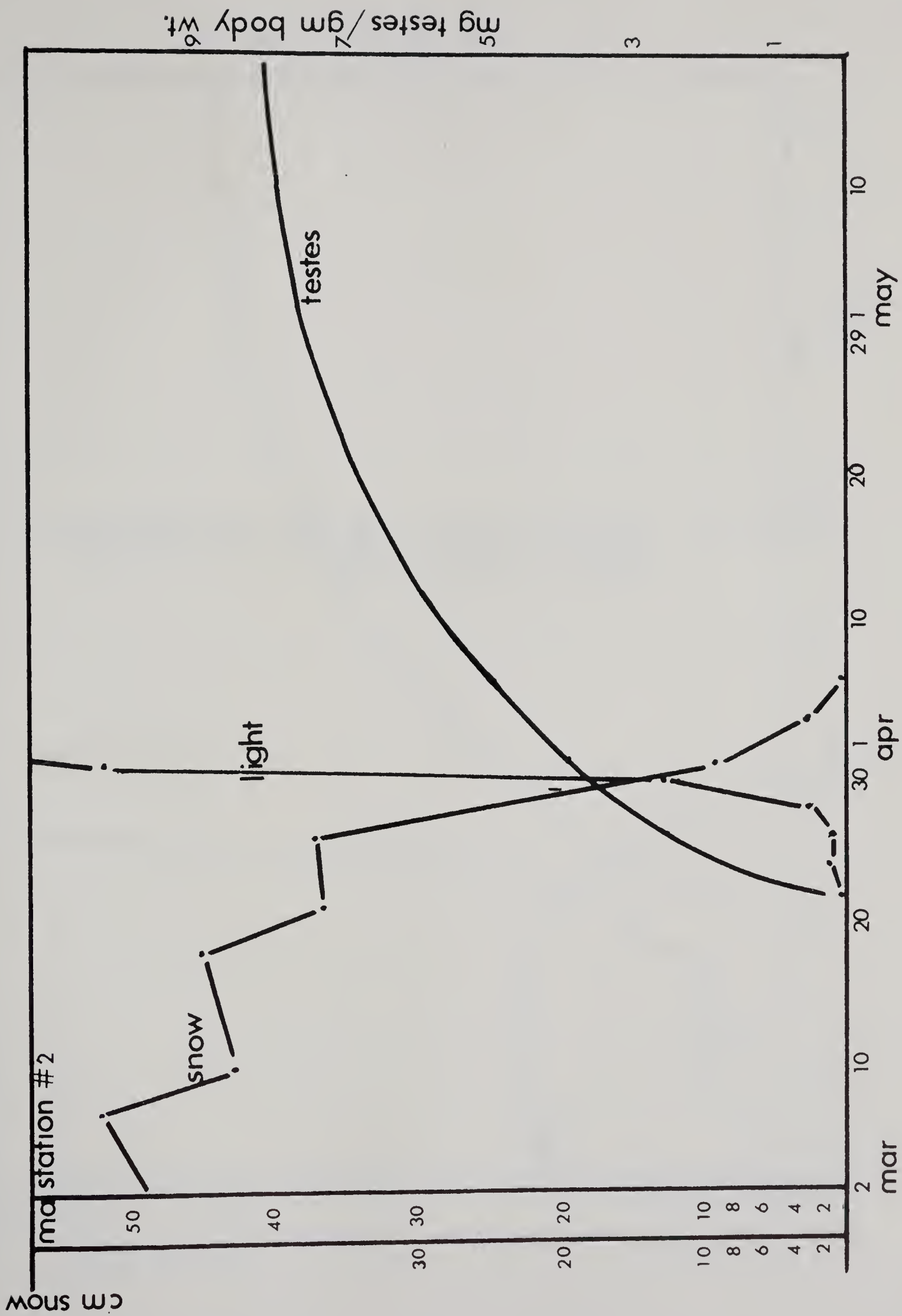


Figure 27. Testicular growth curve of wild population shown in relation to light and snow depth changes at station #3.

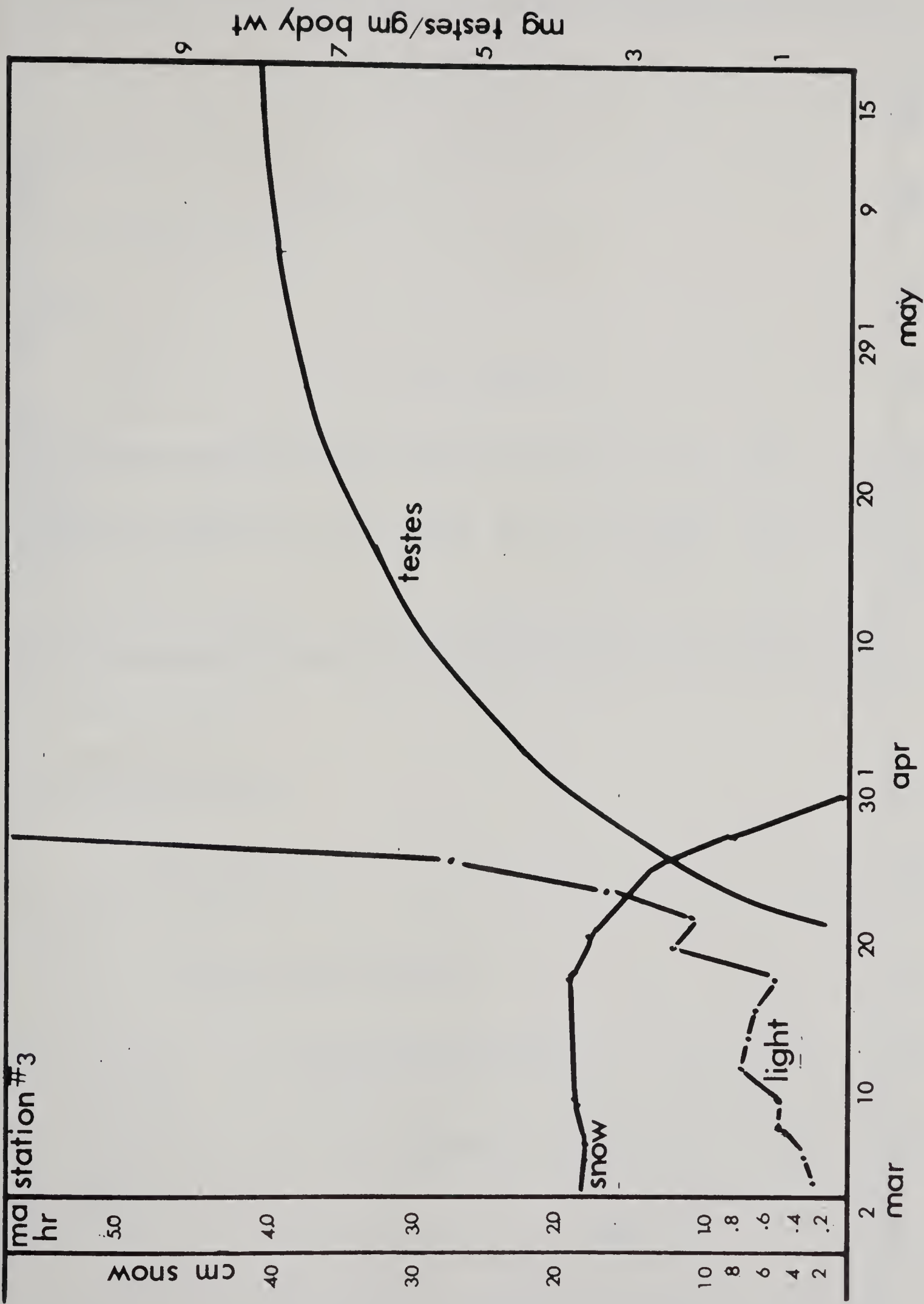
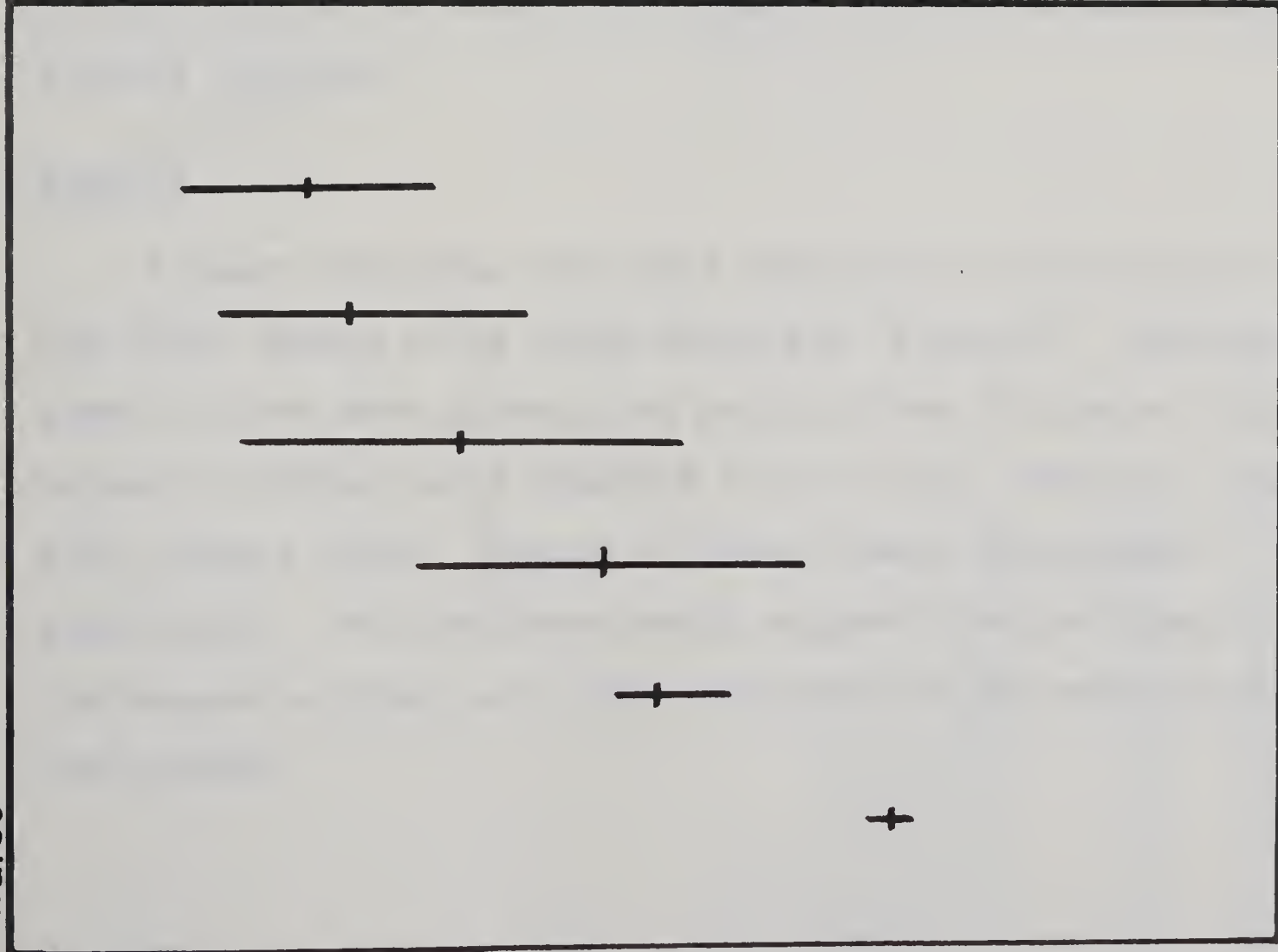


Figure 28. Changes in body weight of wild male animals.

Figure 29. Changes in body weight of wild female animals.

males

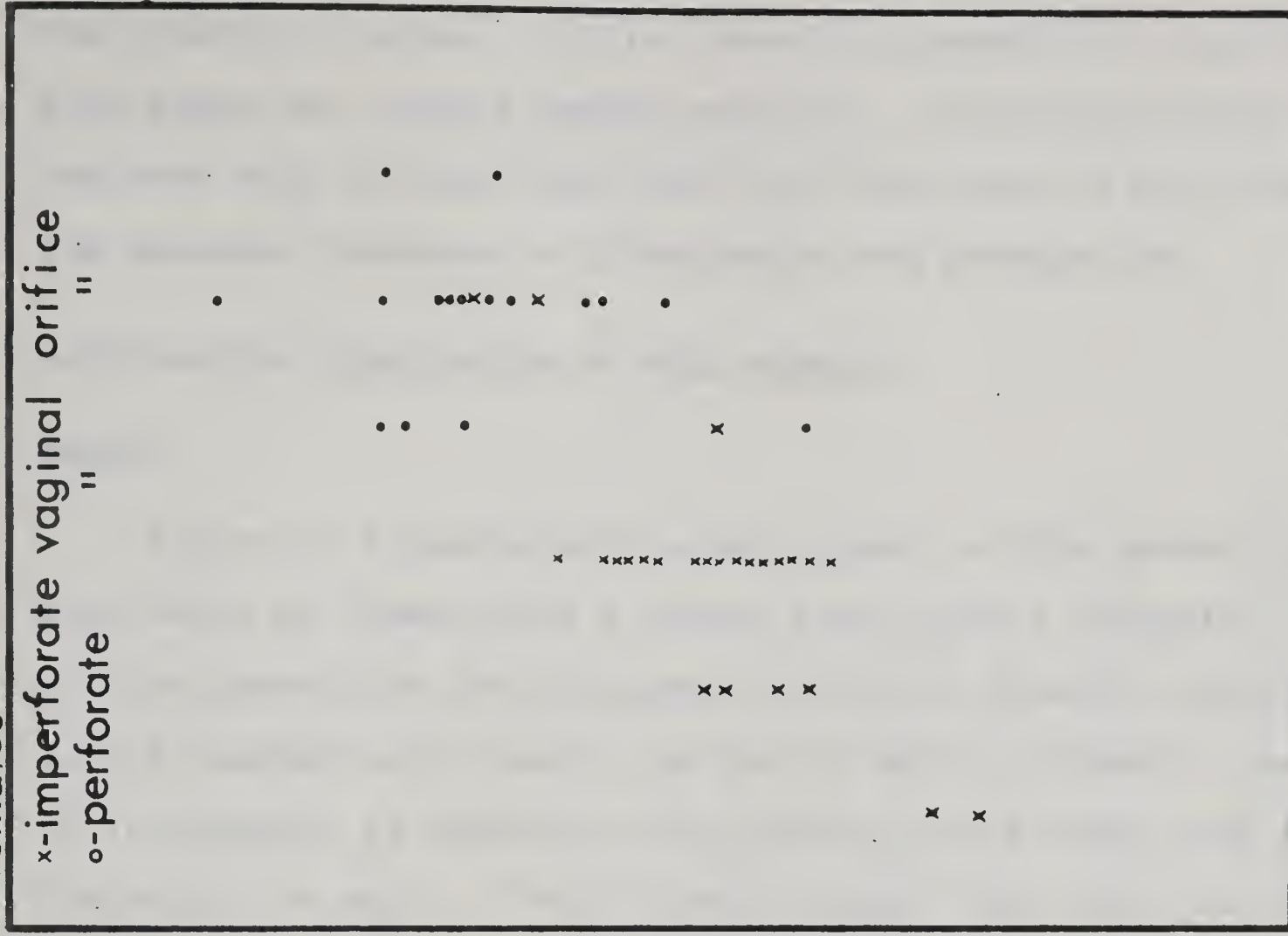
Σg



Feb Mar Apr May
1-15 16-31 1-15 16-30 1-15

females

Σg



Feb Mar Apr May
1-15 16-31 1-15 16-30 1-15

was evident in males. It also shows the remarkable synchrony with which the females became perforate. Perforacy occurs in the same week in which was found the last trace of snow and the greatest increase in illumination and photoperiod.

HISTOLOGICAL EXAMINATION OF WILD SAMPLES

Males

Figure 30 illustrates the development of the testes of wild males as viewed from a purely histological viewpoint. It will be noted that the attainment of actual breeding potential is not reached until nearly the end of March (26 March), and it is doubtful if breeding could actually have begun much before the middle of April. Thus it would appear that males did not precede females in sexual development as much as testis weight figures indicate.

Females

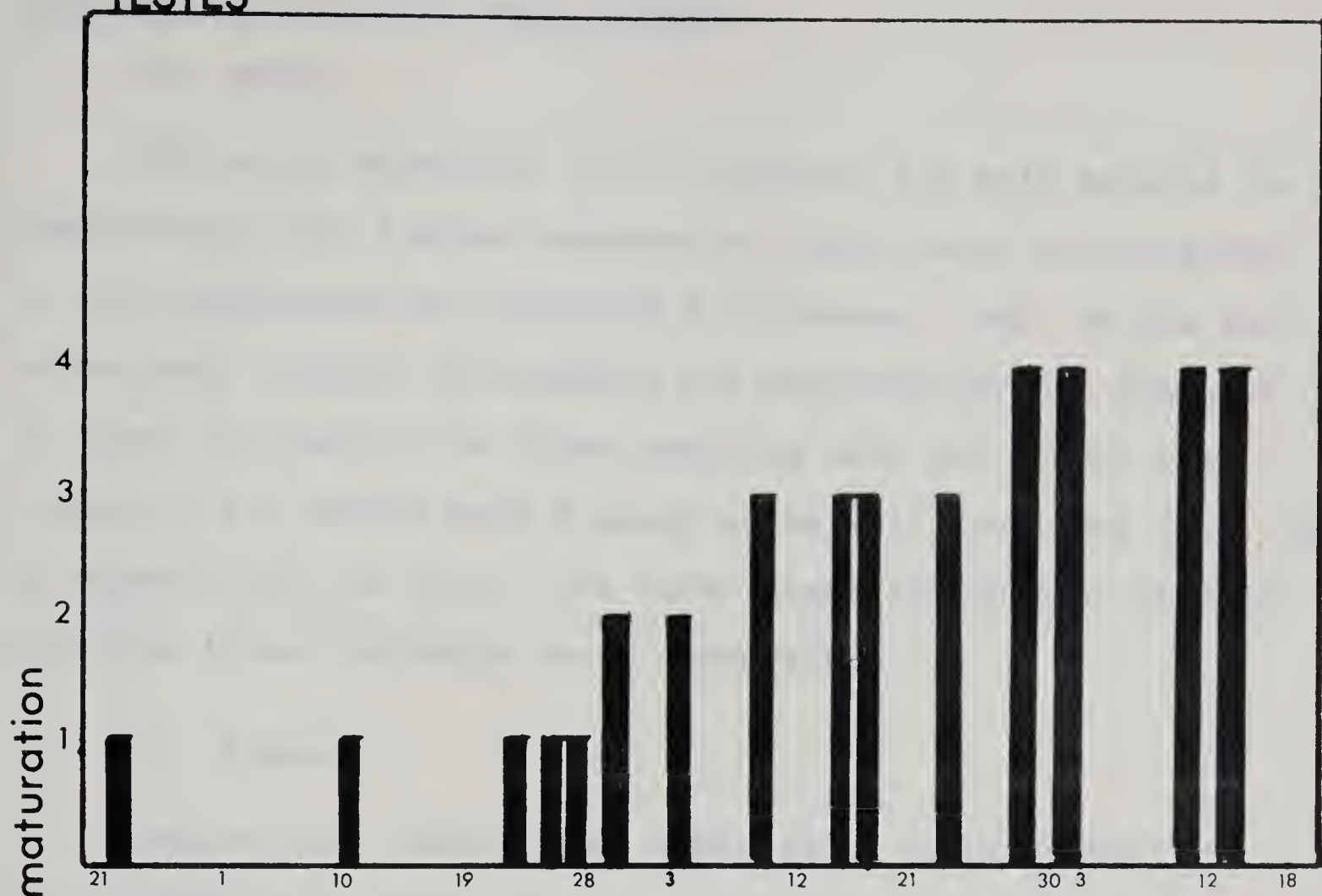
Primary follicles only were observed in the ovaries of the first female to be found perforate (5 April). Development seems to have been gradual and regular from this date, with mature follicles being observed from 23 April onwards, along with corpora lutea. Figure 31 shows female development graphically. This evidence would suggest that perforacy of the vaginal orifice is a good indication of the activity of the ovaries.

Figure 30. Degree of testicular development as judged by histological examination.

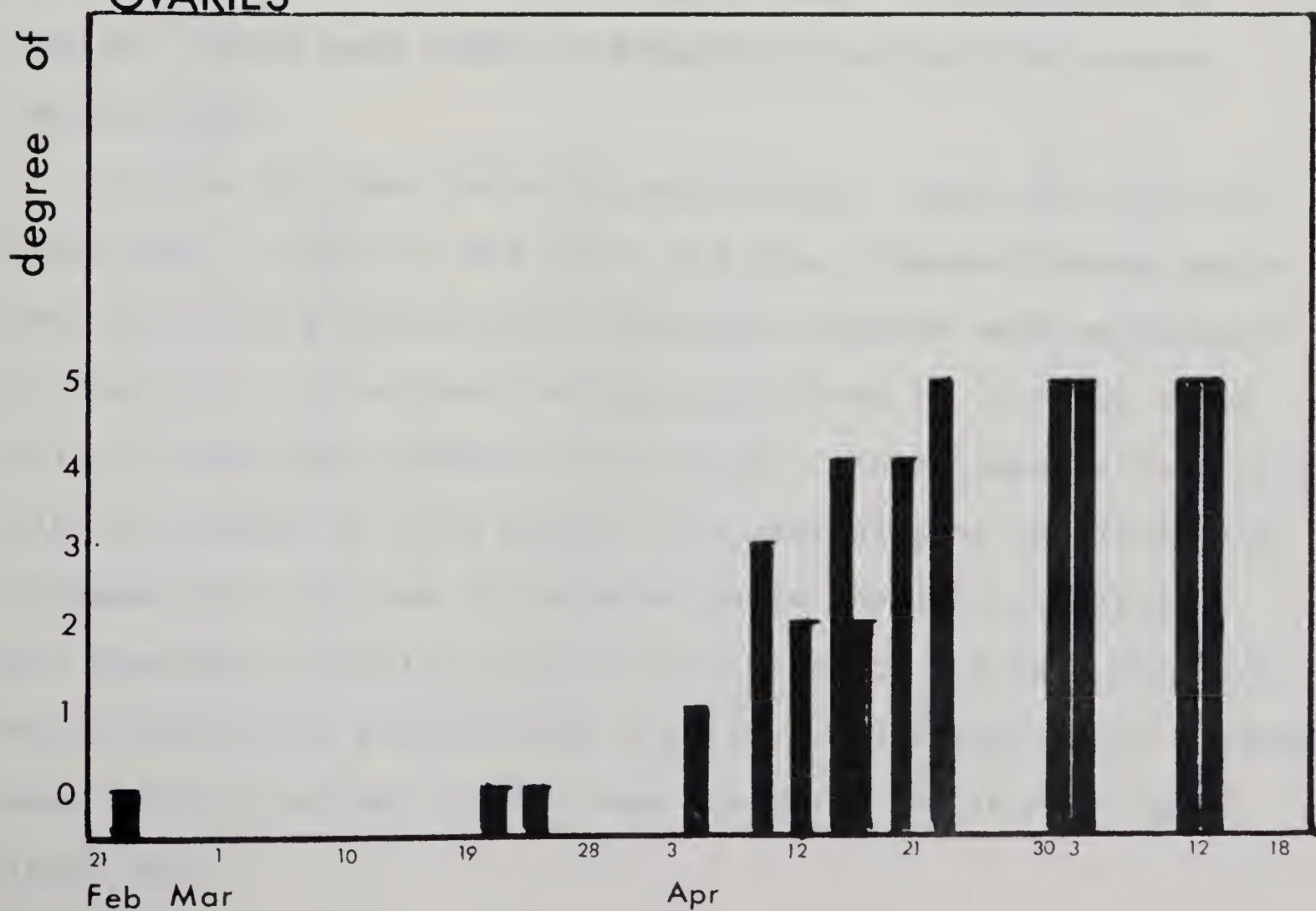
Figure 31. Degree of ovarian development as judged by histological examination.

For Figs. 30 and 31, each bar represents a single animal. For explanation of units, see text p. 23.

TESTES



OVARIES



LABORATORY EXPERIMENTS

Response to Different Wave Lengths

(a) Males

With prior knowledge of the tendency for male mammals to demonstrate only limited response to light, most of the space in this experiment was reserved for females. And, in the few males used, initial development was unfortunately not detected in time, so that by the first sampling date (20 March) the testes in all groups were already quite well developed (Fig. 32). It appears that in this, like other mammalian species studied, the male is not strongly photo dependent.

(b) Females

Females were judged to be approaching sexual maturity when the vaginal orifice became perforate. Following this, vaginal smears were taken to determine when regular estrous cycles began.

Figure 33 shows dates of perforation. Note that all but one animal in each of the white and blue chambers became perforate long before the day that perforate females were encountered in the field. The first perforacy occurred on 15 March after only 19 days under 16L/8D illumination. This compares favorably with the length of time between the beginning of the intensity increase and the time of perforation in the wild population. Two remaining animals, one each in the white and blue chambers, were found to be perforate on 4 April. Their small size suggested poor health, and may in part explain their lag in development (Fig. 34).

Figure 32. Degree of development in experimental males as estimated by testis weight.

W = white light chamber
B = blue light chamber
R = red light chamber

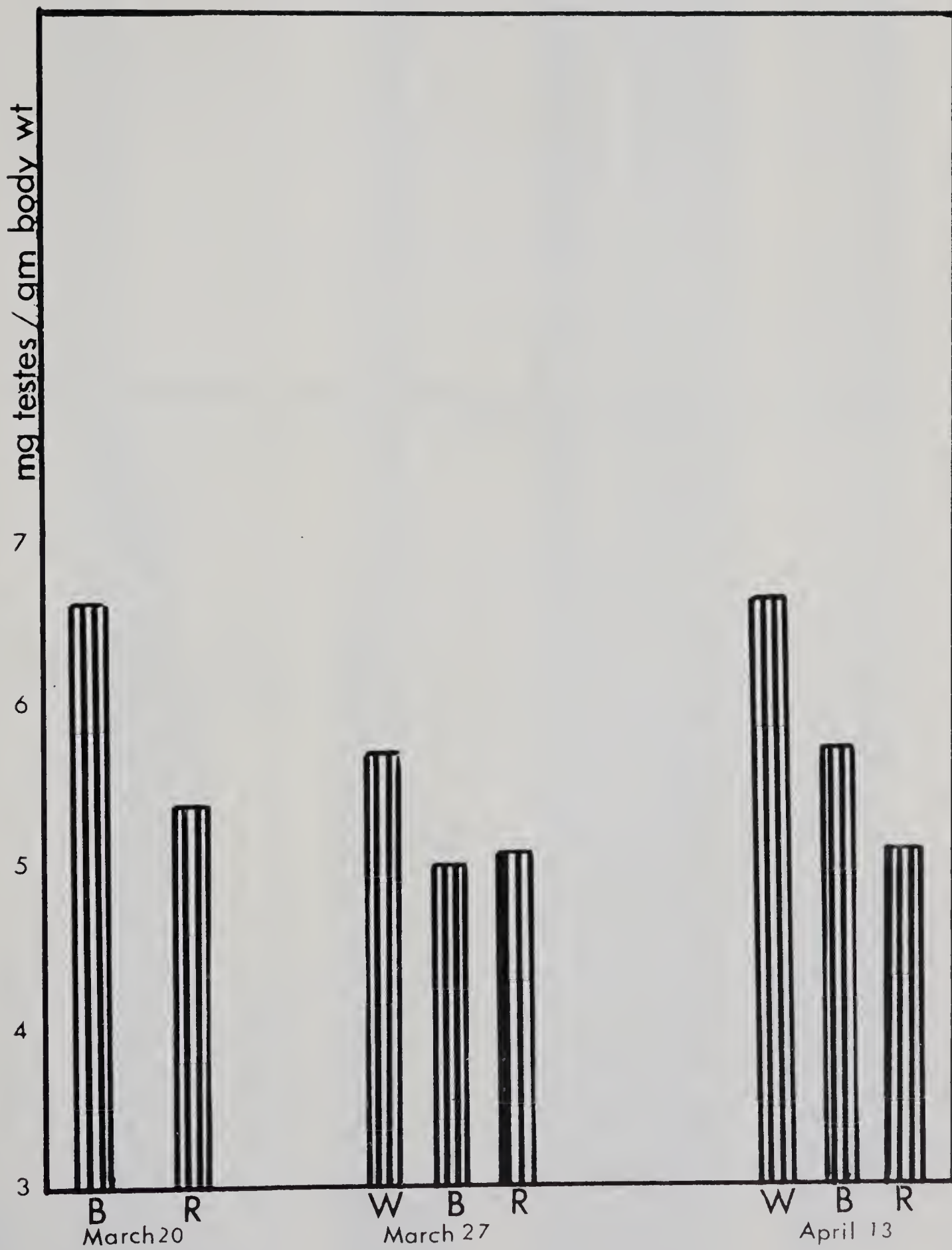



Figure 33. Dates at which experimental female animals become perforate.

 - Imperforate

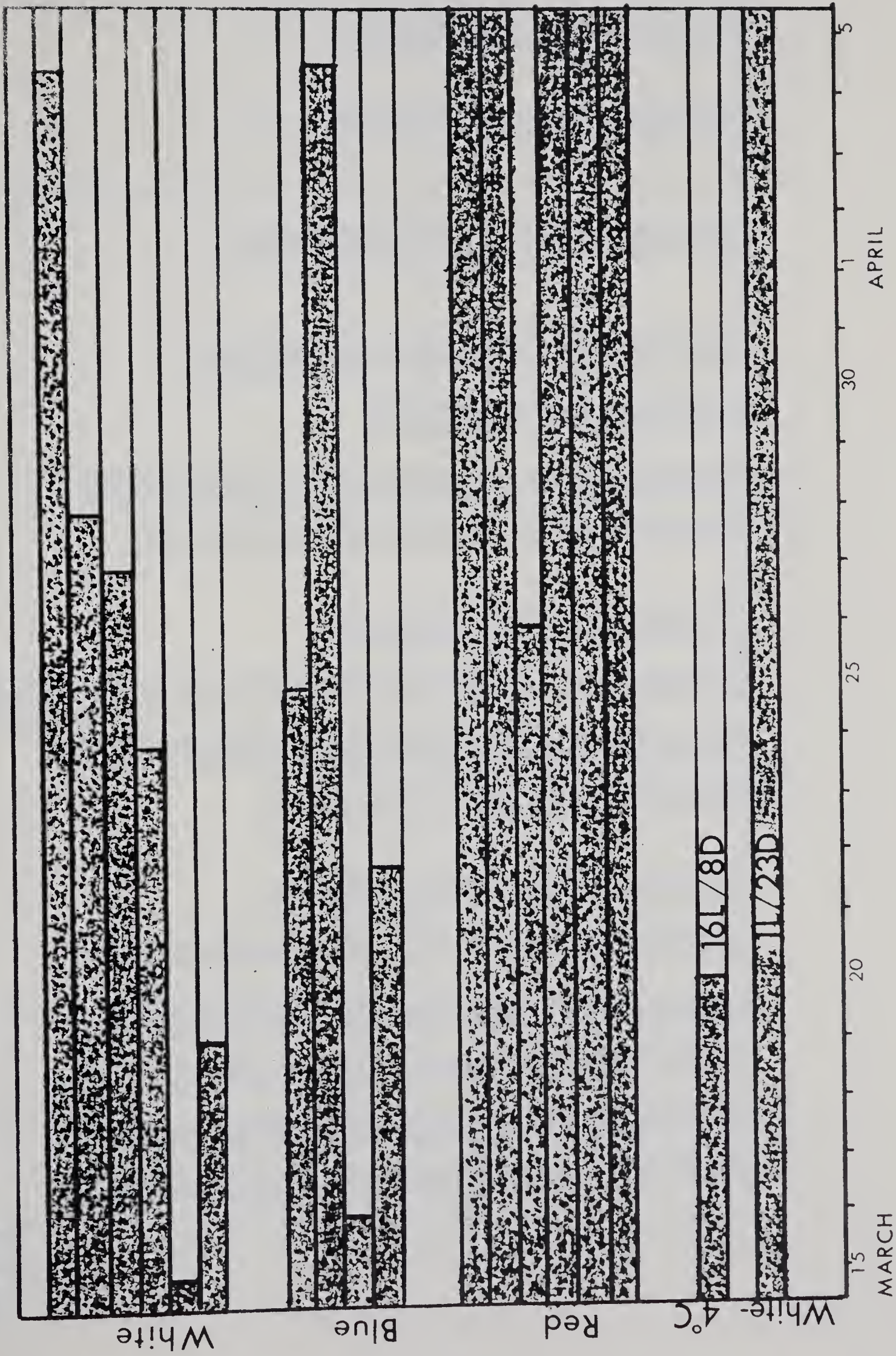
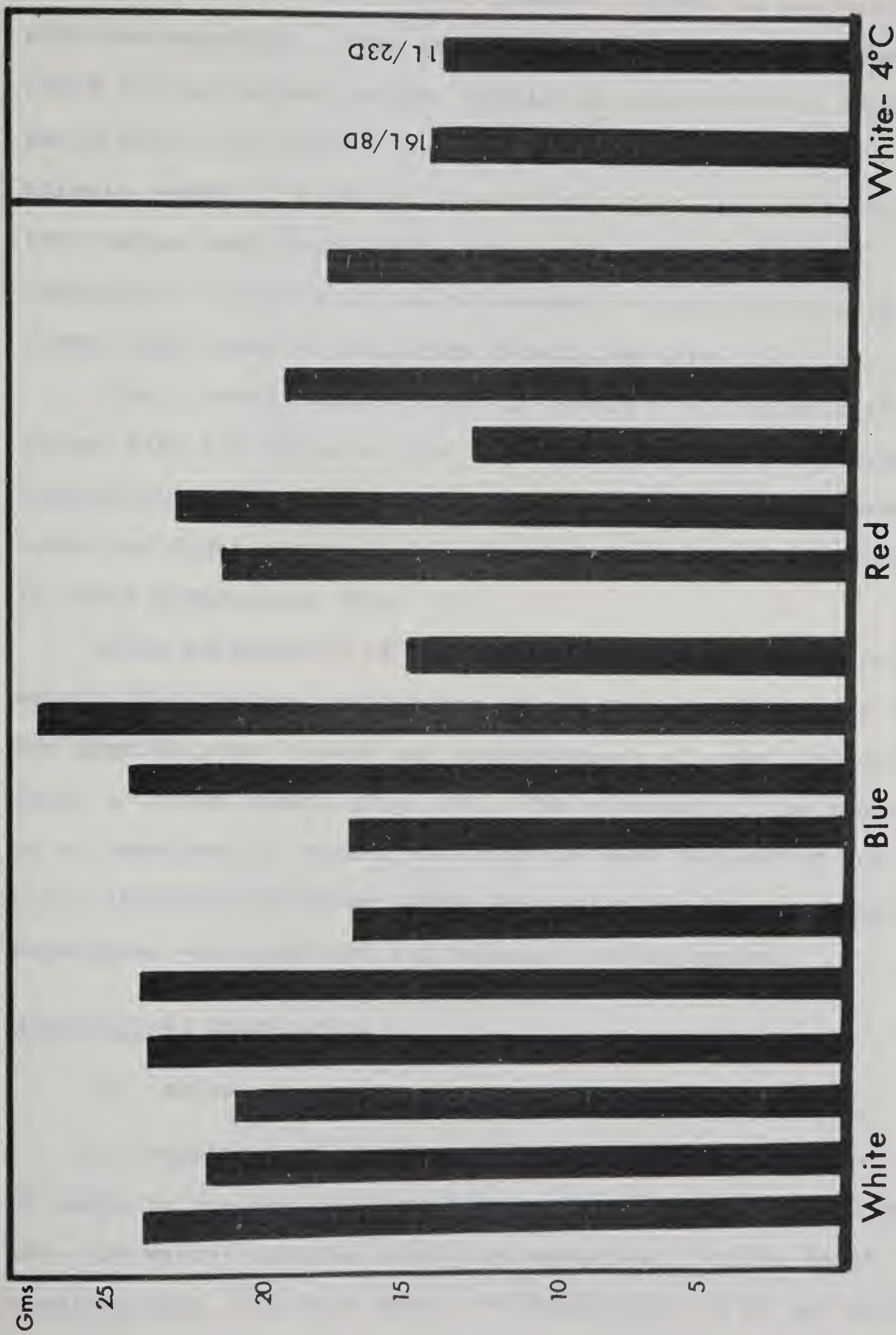


Figure 34. Weights at autopsy of all female animals used in lighting experiments.



The females in red light, however, showed no perforation, with one exception. (One other animal showed slight signs of fluid in the vaginal region, usually an indication of impending perforation, on 2 April, but did not actually perforate). The animals seemed of adequate size to be mature, but on autopsy the ovaries were found to be very small and smooth, as compared to the control (white chamber) animals whose ovaries showed many Graafian follicles developing (Fig. 35).

Thus it would appear that, in general, all animals illuminated with dim white or blue light for 16 hours a day were induced to mature earlier than those in nature, while those under red light of equal intensity and duration were retarded in their development (Fig. 37).

After perforation of the vaginal orifice, it was usually several days before indications of cycling were discerned. A few females never showed any preponderance of cornified epithelial cells in their smears (Fig. 36). The plugging of the vagina of an experimental animal was taken to mark the end of the first cycle (Rowlands and Bramble, 1936). When plugging became general, the experiment was ended and all animals were autopsied.

Histological Examination

(a) Males

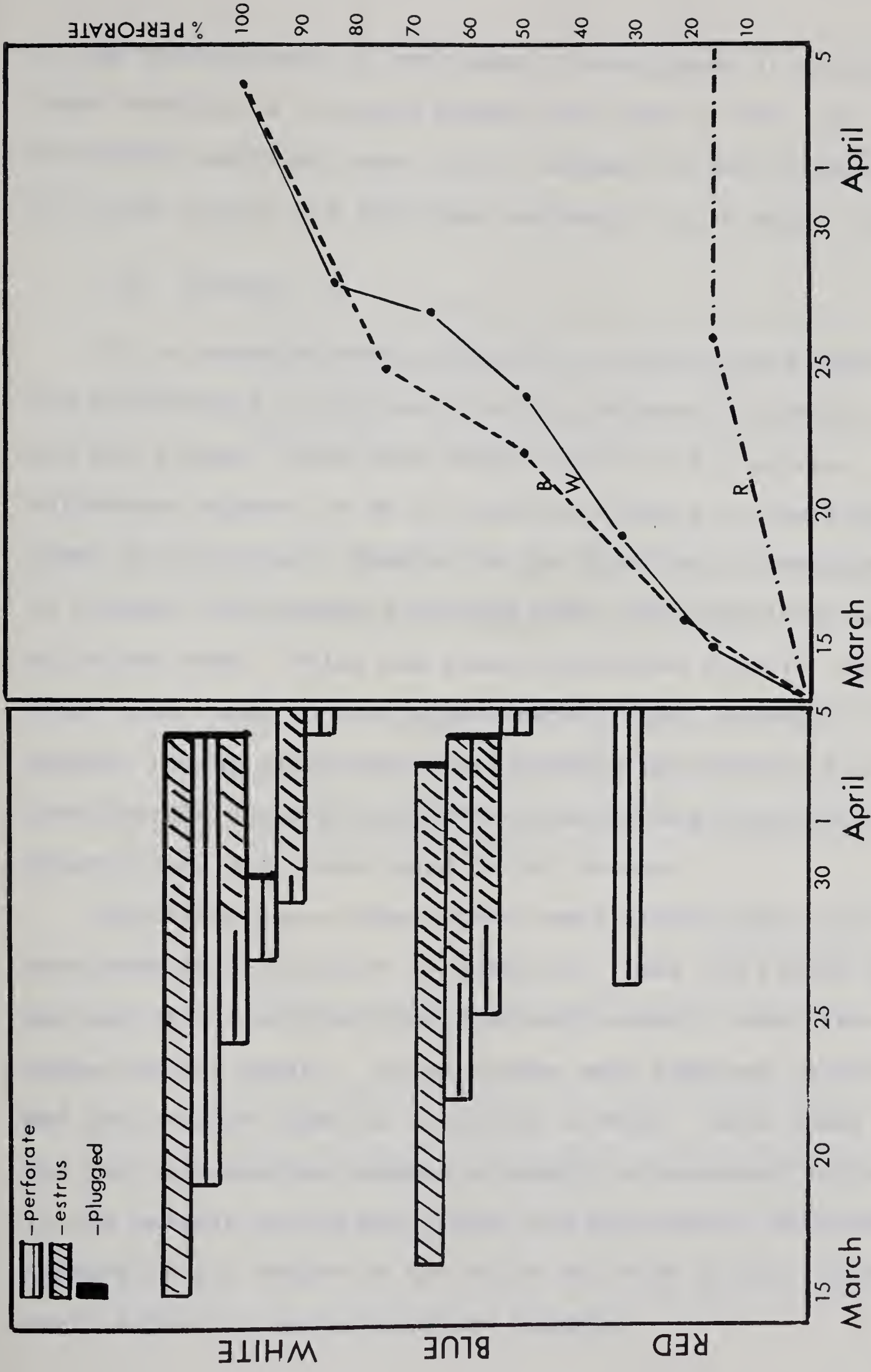
All experimental males were found to have large quantities of sperm in the seminiferous tubules from the first sampling date (20 March) onwards, with one exception. On the first sampling date, the male under low temperature (4 C) and short day (1L/23D) showed no development. Unless this is attributable

Figure 35. Ovaries from females in red (above) and white (below) light.



Figure 36. Dates of perforation, dates of first indication of estrus, and dates of plugging for all experimental females.

Figure 37. Percentage of all females in each group showing perforate vagina at each date of examination.



to the idiosyncrasy of one animal, development in animals under these conditions occurred between the time of the first and the second sampling dates (i.e., between 20 and 29 March), while all other groups had developed maximally by 20 March (Fig. 38).

(b) Females

It is somewhat more difficult to evaluate and describe the differences in ovarian histology between the White, Blue, and Red groups, since many stages occur in all groups. The difference appears to be in relative numbers of the several types of follicles. Females in red light had a preponderance of primary and growing follicles with only occasional maturing or mature ones. White and blue-illuminated animals, on the other hand, seem to have approximately equal numbers of all stages, having relatively fewer primary and growing follicles than the Red group but more of the maturing and mature follicles. Atretic follicles were found in all groups.

While the above observations were subjectively obvious, they were more difficult to quantify. Data for Figure 39 were derived from a single slide from each animal, taken from the center of the series. These slides were examined carefully and the various types of follicles counted. Both these counts and the illustration suggest a paucity of advanced follicles in the animals of the Red group, and more nearly balanced numbers of all stages in the White and Blue groups (as one would expect in sexually mature animals).

Figure 38. Degree of development in experimental males as indicated by histological examination.

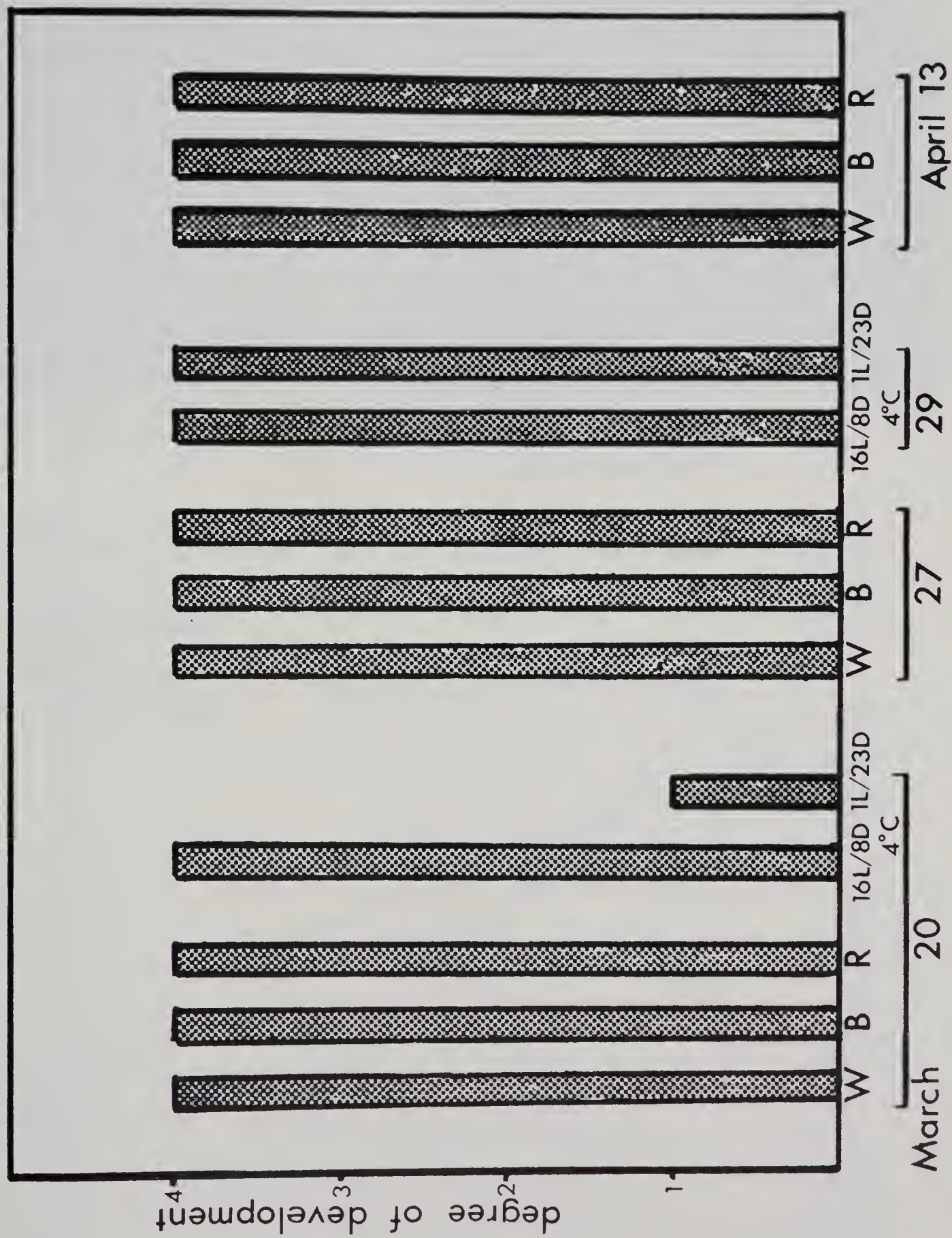
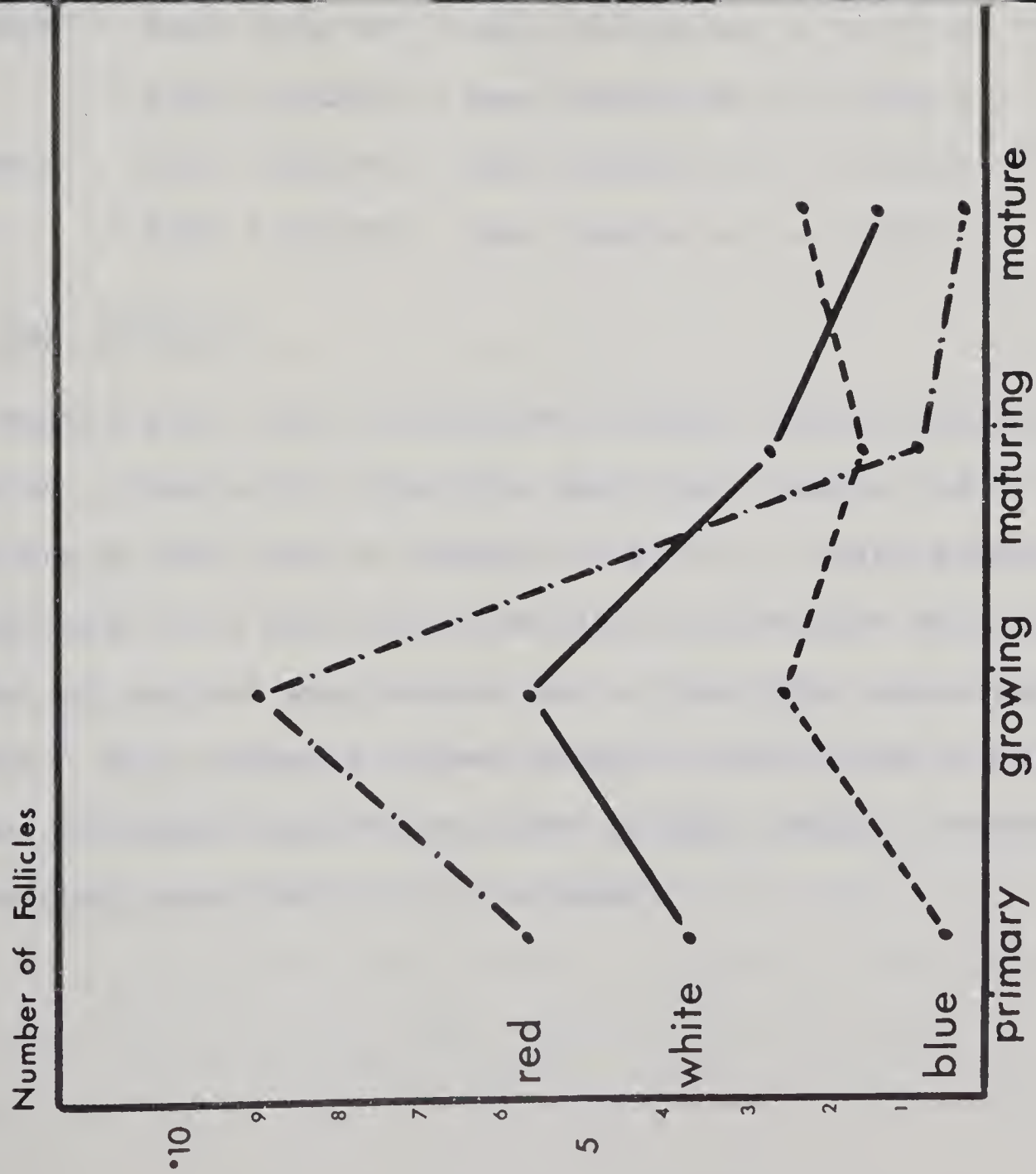
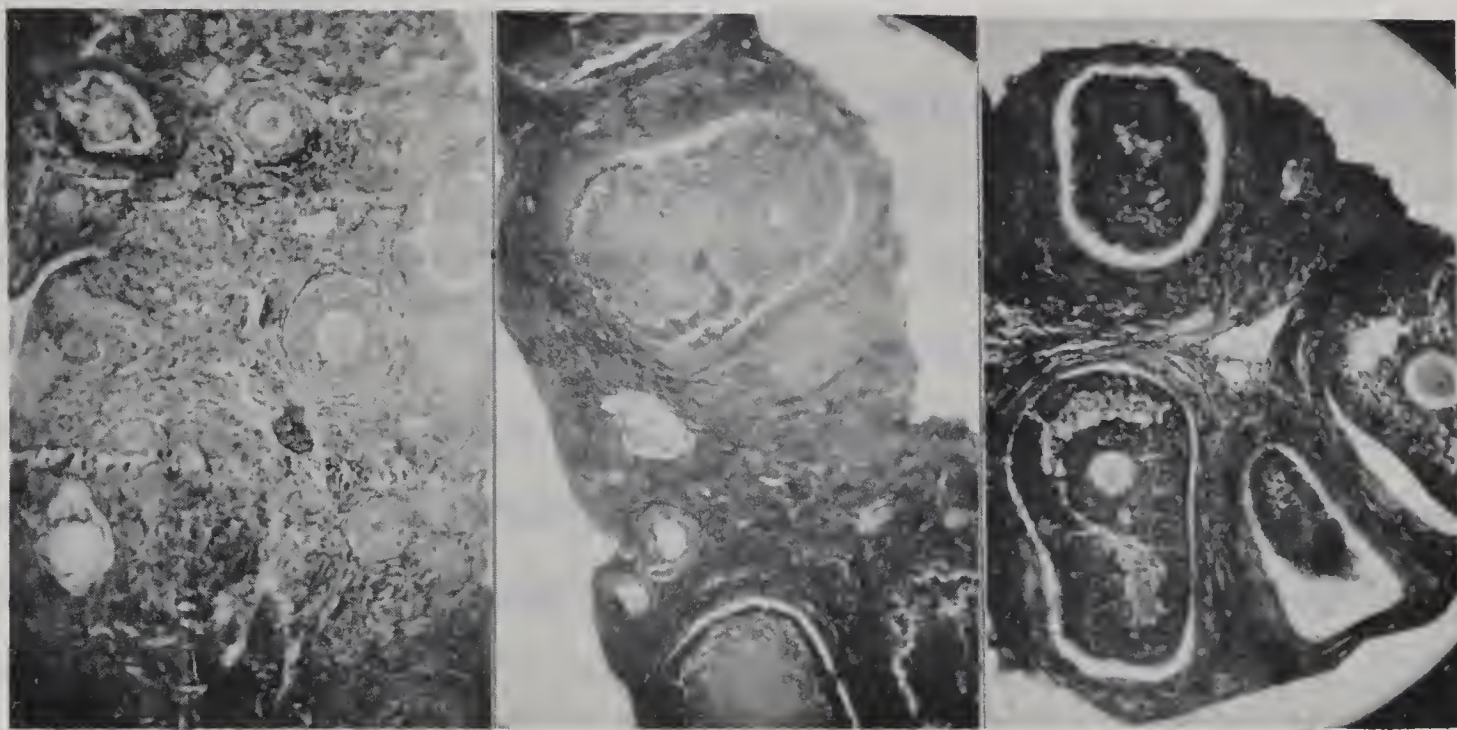


Figure 39. Degree of development in experimental females as estimated by the numbers of the various type of follicles observed in histological examination.

Top line and photograph - animals from red light

Middle line and photograph - animals from white
light chamber

Lower line and photograph - animals from blue
light chamber



Response to Light While Under Refrigeration

(a) Males

At the first sampling date (20 March), the male from the long day (16L/8D) chamber showed testes twice as large as those of its counterpart from the short day (1L/23D) chamber. However, by the second and final sample, 29 March, very little difference was discernible. Thus it would seem that under low temperature conditions, a long photoperiod produced only slightly faster development in the male, as was indicated from the wave length test.

20 March:	#126 (16L/8D) - mean testis wt. = 0.137 g
	#129 (1L/23D) - mean testis wt. = 0.076 g
29 March:	#127 (16L/8D) - mean testis wt. = 0.176 g
	#130 (1L/23D) - mean testis wt. = 0.160 g

(b) Females

Female #128 from the long day chamber became perforate on 22 March. Female #131 from the short day chamber did not perforate by the time of autopsy (6 April). These animals weighed only 13 g each, and thus did not show the weight gain evident in natural populations and in the other experimental animals. This suggests higher metabolic drain due to cold stress, although food was provided ad lib. Males, however, all weighed more than 20 g at autopsy.

Color Preference

Figure 40 demonstrates the preferences indicated by total number of entries into each of the respective color chambers, and also the more conservative picture of "number of 10-minute intervals containing entries". In both figures, preferences are indicated by percentages of total entries attributed to each color. By chance alone, one would expect 8.33% of all entries to be attributed to each color. Some colors received more attention than would be expected by chance alone, although only the black chamber received a significantly greater number of entries, by either method of evaluation, at the 5% level (at the 10% level, both black and red are significant in the total entries evaluation, and only black by the 10-minute interval method).

There seems to be a trend toward avoidance of light. Judging from the observed inability of the mice to avoid capture under red light, one can assume that they see rather poorly under these long wave lengths. Therefore the chambers favored (black, and possibly red and infra red) may be interpreted as attempts at light avoidance. The mottled chamber also received some attention, possibly because it successfully simulated the effect of overhead branches of shrubs and so suggested the security of cover to the animals. The avoidance of light may also be interpreted as an attempt to remain under cover, as would be expected from the results of Mossman (1955). Mossman measured cover by using light intensity as an index, and found a great preference by the small mammals for the low intensity

(i.e., well covered) areas.

Therefore, the observed color preferences may represent merely attempts to avoid light and so stay under cover. A similar tendency in nature could possibly discourage animals from coming to the snow surface during winter or spring, and thus contribute to their lack of awareness of atmospheric light conditions. However, while this experiment seems to indicate light avoidance by the voles, it must be reiterated that intensity differences could not be controlled when using these filters, and that the results may therefore be complicated by this shortcoming.

Figure 40. Indications of color preferences.
Bars represent averages obtained by
pooling the results from all 20 voles
used in the experiment.



DISCUSSION

As noted previously, many microtine rodents have been demonstrated to be responsive to artificial lengthening of the photoperiod (Baker and Ransom, 1932; Cowan and Arsenault, 1954; Pinter and Negus, 1965; Lecyk, 1962; Whitaker, 1940). The differential response of female C. gapperi to wave length and photoperiod suggests that this animal is also reproductively photosensitive. As has been found with all mammals studied to date, it would appear that the female red-backed vole is more affected by light than is the male. Weight gains associated with gonad development in both sexes caution that nutrition may be closely associated with sexual maturation as well (see also Pinter and Negus, 1965).

It is not surprising to discover that the microtines' visual system acts as a receptor to external information not directly concerned with vision; in fact, the system does not seem to be designed as a strictly visual instrument at all. Milne and Milne (1962) state that

Vision serves the mouse chiefly in warning it of the approach of an enemy. To help see in all directions simultaneously, the mouse's eye has a greatly enlarged lens that is so nearly spherical as to give the eye periscopic vision. There is no need to focus on anything. Instead, the eye sees poorly from horizon to horizon. It is extremely sensitive to any change in the panoramic field, and warns the mouse to freeze, lest movements or sounds betray its position.

Similarly, Roberts and Drew (1939) say of the rat that "vision ... would appear to be for the general orientation of the animal, and not the identification of specific objects".

The significance of these two references is that they demonstrate that the nature of the rodent eye is such that it will draw in light from horizon to horizon, with no particular concern for extreme definition of individual objects. It seems to be rather more a glorified photosensor than a visual organ as we usually think of it. Furthermore, the great preponderance of rod cells over cones again suggests an emphasis on photoreception rather than image forming. However, the increased sensitivity gained through an all-rod retina may also restrict the range of wave lengths to which the animal is sensitive. My observations under red light suggest that, judging from the animals' complete failure to move to avoid capture, they are incapable of perceiving red light visible to humans.

I have previously mentioned the significance of three environmental factors, food, light, and temperature, to the reproductive processes of mammals. I feel it is important to realize the uniqueness of light in this trio. Temperature can impose considerable metabolic stress on a small mammal, causing it to use all available energy simply to maintain the body temperature. Such a circumstance would clearly exclude reproduction. Similarly, a shortage of nutrients can restrict the amount of energy available for reproduction. It would appear that both low temperature and nutrition are limiting

factors with respect to reproduction.

Light, however, is unlike the other factors discussed in that it stimulates rather than limits reproduction. One may presume that a prerequisite to the success of this stimulus must be that the animal has sufficient energy available. However, given this prerequisite, light appears to be effective in initiating the onset of breeding. Hammond (1954) discusses the relationship of the three factors thus:

As a synchronizing agent, light has the merit of much greater regularity of fluctuation and thus, teleologically, might be expected to be a fundamental common regulator. On the other hand, [since] factors such as temperature are of more immediate importance, it is not odd to find them acting as regulators, or moderating light-regulation.

There is some question, I believe, as to whether or not the temperature in the subnivean environment is ever low enough to constitute a negative force with respect to breeding. It is clear in the present study that development and probably actual breeding had commenced long before mean temperatures had begun to rise in the voles' microclimate. Not only were the animals at temperatures near freezing all winter, they must remain at about this temperature until all snow and ice is gone. Even after this time, there is little rise above this mean until the end of April, by which time litters are beginning to be born. The animals were therefore breeding at temperatures roughly equivalent to those which they had

experienced all winter. This observation is supported by the success of the animals retained at 4 C in the laboratory. All animals in long-day conditions became mature at the same time as the other experimental animals (except those in red light) and in advance of the natural populations (still under shorter photoperiod). Furthermore, Baker and Ransom (1932), Whitaker (1936) and Hart (1951) all observed the stimulatory effect of light for mammals irrespective of the presence of normal winter temperatures. Baker and Ransom also noted (1933) that in the wild, the duration of the breeding season increases with latitude, as does photoperiod, whereas the reverse is true with respect to temperature. However, it must be realized that this study was done on voles in Great Britain. In view of the continuous breeding of tropical mammals, the conclusions of Baker and Ransom certainly cannot be extrapolated to apply to animals from all latitudes.

No doubt, low temperature may, under some circumstances, thwart all attempts at reproduction because of high energy demands, through actual mortality, or through inhibition of ovulation (Quay, 1960). But, due to the stability of the subnivean temperatures in the taiga (Pruitt, 1957 and 1963; Formozov, 1963; Geiger, 1950), it seems highly unlikely that low temperature exerted such an effect on the animals in this study and it seems even more unlikely that increase in temperature was great enough or occurred early enough to play any role in stimulating gonadal development in the spring. It is possible, however, that moisture derived from melting snow in early spring is instrumental in the germination of seeds

under the snow, which could have profound nutritional benefits to microtines.

The fact that adverse temperature can discourage breeding emphasizes the interaction between meteorological and physiological factors, and the futility of trying to single out one factor as the major one. It seems most probable that in a given year a number of factors may be involved. In the case of light and temperature, great depths of snow stabilize temperature but obscure light; shallow snow permits light penetration but allows temperatures to fall. Which is more important? The problem is not critical perhaps in forest situations, such as those of the present study, but may be very important in the tundra. It may be that light acts as a stimulant only if the temperature is high enough to permit the necessary expenditure of energy. That is, low temperature may limit the response of the animals to the light stimulus. This delicate balance and the resultant dichotomy of response may lead to selection of animals which are not very responsive to either factor. This suggestion was made by Schwartz (1963) with respect to northern microtines and problems connected with it are discussed below.

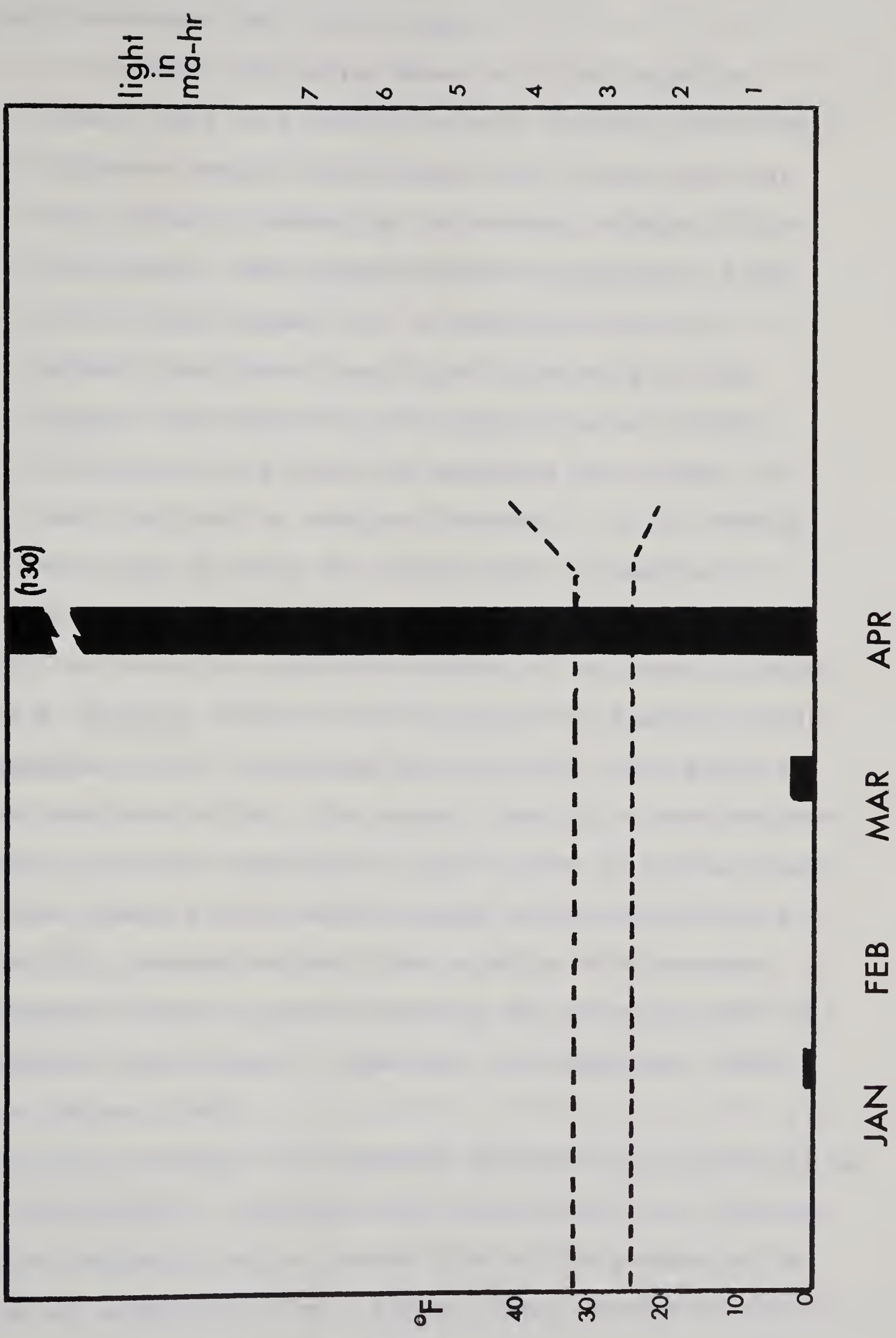
Nutritional requirements throughout the winter are probably reduced somewhat through the moderation of temperature by the snow cover. But it is clear that certain key nutrients, such as vitamin E, must also be present if the animals are to breed.

I have suggested that food may be sufficient and the temperature at a satisfactory level to support reproduction long before breeding actually occurs (observations of winter

breeding under the snow by Microtus pennsylvanicus (Hamilton, 1937) and of continuous tundra breeding in Lemmus lemmus (Krebs, 1964) support this opinion). Light is the variant which would best herald the approach of spring and the optimal conditions for the rearing of young. In fact, it may be that of the three environmental variables mentioned light is the only variant at the time at which breeding usually begins. (Figure 41 shows diagrammatically the comparison between light and temperature changes at the onset of the breeding season). But the question invariably arises as to whether or not the animals would eventually breed without any external stimulus at all.

The answer appears to be yes, at least under some circumstances. Breeding under the snow has been reported several times. Lecyk (1963) observed that "In spite of being kept under short-daylight conditions ... the Field Voles started breeding only one month later than the control animals." Lecyk reports that Polyatov, working with the same animal (Microtus arvalis) observed no delay even when animals were maintained in total darkness. Hill and Parkes (1934) obtained similar results with the ferret, although these results were questioned by Bissonette (1935). Hammond (1954) reported confirmation of the results of Hill and Parkes, but Marshall and Bowden (1934) were able to suppress development by total darkness in all ferret females except those that had already begun to develop at the beginning of the experiments. (Bissonette felt that starting the experiments too late was the explanation for the observations of Hill and Parkes also).

Figure 41. Variations in light and temperature throughout the late winter and early spring. Solid bar indicates average light readings at station #2. Dotted line indicates an approximate range of temperature in the subnivean environment.



Lecyk expresses the opinion that;

... in most free-living mammals of the temperate zones, there is a certain natural internal periodical rhythm of sexual activity and rest. This cycle has been probably induced by the seasonal changes of the environment, then fixed and made independent of the factor that induced it. In the field vole, it probably manifests itself most vigorously in the spring, and therefore it is impossible to inhibit breeding in this season by exposing the animals to short daylight or complete darkness. It is, however, very easy to bring the field voles to breeding in autumn-winter season by lengthening the daylight.

So while confirming the positive effects of increased illumination on M. arvalis, Lecyk is more willing than Hammond (1954) or Bissonette (1935) to presume the existence of so exact an internal synchronization. The general feeling of most workers on mammal (and bird) responses to light seems to be that there is a crude internal cycle which depends on "external factors ... to bring this internal rhythm 'into relation with seasonal environmental change in such a way that the young are born at a favourable time of year' " (Marshall, in Zuckerman, 1962; see also Farner, 1964).

The light stimulus is therefore regarded as a synchronizing agent ("Zeitgeber"). Breeding will occur without it, but with much less regularity and a greater risk of the production of young at an inopportune time. Farner (1964) emphasizes the evolutionary importance of selecting the most reliable and most

regular external stimulus, and he suggests that under most circumstances light would fit these requirements. (The effectiveness of light is at least questionable with respect to tropical and subterranean species (Zuckerman, 1962)).

While in agreement with this consensus, I feel that the modifying effect of snow changes the magnitude of the light stimulus considerably. For while all temperate zone animals are subject to light increases, none but those inhabiting the subnivean environment are subjected to changes of this order. The results of this study show that the animals normally receive an increase of at least a thousandfold in illumination within the period of only one or two weeks, while the snow is disappearing. During this time, temperature level (Longley, pers. comm.) and food supply remain virtually the same as they had been all winter (although, with the onset of melting, there is the possibility of some seeds, those which do not require heat, germinating. This certainly merits further investigation). It would seem at this time that to all intents and purposes, light is the major, if not the only, variable. And, it is varying not subtly but dramatically. Moreover, the effects may well be even more dramatic than the selenium cells would indicate, for in fact, there appears to be a preponderance of light from the red end of the spectrum in the subnivean environment. And while the selenium cell is slightly more sensitive to these wave lengths than is the human eye, the rodent eye appears to be virtually blind to red light. This realization is in keeping with the differential effect of wave length demonstrated in the laboratory, which clearly indicated

that the blue end of the spectrum was stimulatory, whereas animals in red light, even when given ample foodstuffs and slightly higher than normal temperatures, were slow developing.

It may be fair to regard the red light experiment as one of total darkness, for apparently the animals were not able to perceive shapes. However, one must be cautious in postulating that light is sensed only visually. Marshall and Bowden (1934, 1936) observed that ultra-violet was the most stimulatory of the wave lengths to which ferrets were subjected, implying that some retinal response of non-visual cells is involved.

It should also be noted that the advance in sexual maturity observed in the red-backed vole was induced by light at rather low intensity. If Marshall's observations on ferrets (increasing response to increasing intensity) can be extrapolated to other photosensitive mammals, then we may expect a far greater response by the voles to environmental light.

One should not overlook the possibility that animals living beneath the snow are exposed to light because of their behavioral traits. These animals may come to the surface to feed when atmospheric temperatures permit, but no tunnels to the surface were observed on the study area after February. The results of the color preference experiment strongly suggest that given a choice, the animals will definitely avoid strong light and will by preference feed in dim or totally dark areas. Therefore it is doubtful if animals would often be inclined to expose themselves to atmospheric light.

While, prior to this study, it had not occurred to biologists to expect a shift in spectral composition toward the long wave

lengths under the snow, this fact was suggested by Geiger in 1950.

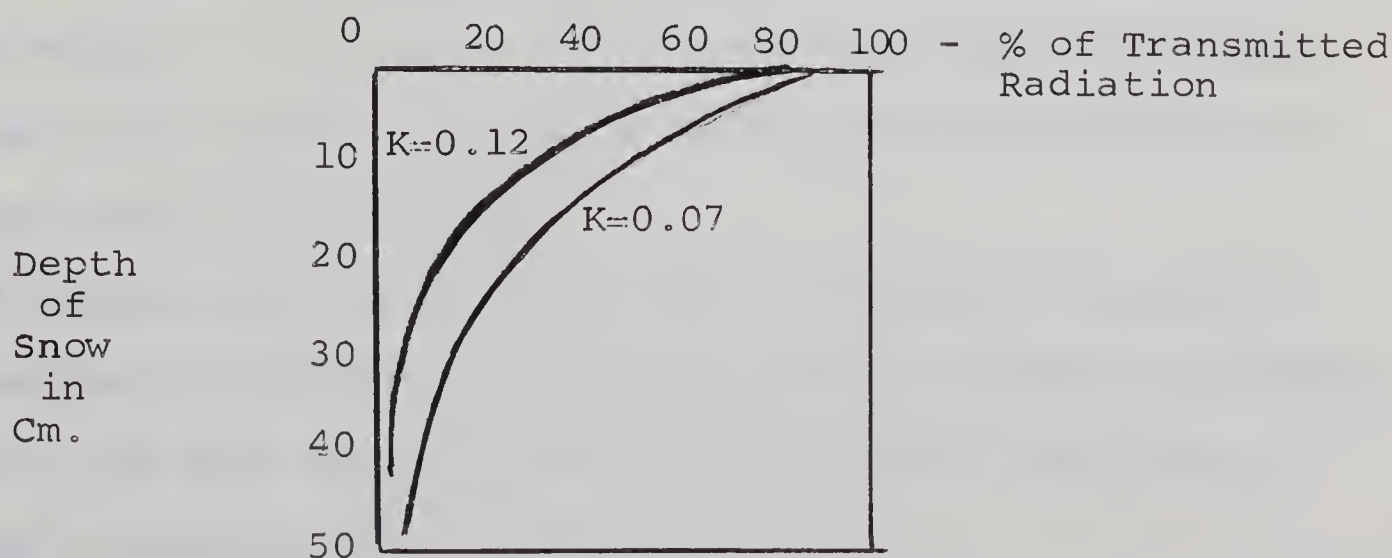
Geiger approached snow study primarily from a supranivean rather than a subnivean viewpoint. He inferred what was present beneath the snow by examining what was reflected above it. Through this method of investigation, Geiger and other German workers reviewed by him have noted that the albedo (reflecting power) of snow usually ranges between 75 and 88% (and occasionally 100%) for newly-fallen snow, and that for infared radiations (around 1000 A) the snow is virtually "black". That is, the snow transmits virtually all the long "heat" waves that hit it, while reflecting the shorter visible waves. Extrapolating from this, we would expect that, of the visible wave lengths penetrating the snow, the longer reds would predominate over the shorter blues and violets. Geiger further reported that the region most completely reflected is the ultra-violet, the region which Marshall has shown to be most effective in stimulating ferrets.

I feel that Geiger's view of the situation can contribute much to the biologist's understanding of the importance of snow. From his purely physical viewpoint, Geiger describes many qualities which are of biological interest. For instance:

In the first place its [snow's] poor heat conductivity results in a crowding of the isotherms near the surface. Deep within the snow, its temperature is only slightly below freezing, even when the air temperature may be as low as -33 C. This illustrates how great protection is afforded seeds by a winter

snow cover. Heat waves penetrate the snow considerably faster than do cold waves, for while the latter are transmitted only by true heat conduction, the former have the benefit of a pseudo-conduction through infiltrating water from melting.

Geiger offered Olsson's formula " $J = J_0 \cdot e^{-kd}$ ", where J represents the total radiation penetrating to a depth of d centimeters, with J_0 being the radiation penetrating the snow surface and k a constant. This simple absorption law is strictly applicable only for an optically homogeneous substance, and is therefore only approximate with respect to snow. Nevertheless, values for K have been obtained which fall between $k = 0.07$ and $k = 0.12$. Using these data Geiger presents the following absorption graph. The difference in k values is due to the fact that "since the long waves are absorbed by the snow, an instrument which is sensitive to longer wave lengths will give a higher k value". Hence a total radiometer (pyranometer), such as those used by limnologists, will give higher k values than one would find using a visual range selenium cell, as in the present study.



Transmissivity of snow cover for radiation (from Geiger, 1950)

Geiger's report illustrated that both the temperature stability and the reduction in visible light in the subnivean environment are dependent on the reflecting and conducting properties of snow, and it appears that it is through a physical study of snow that the best conception of the subnivean environment can be derived.

Considering the physical properties of snow, it is to be expected that the long wave radiation would penetrate more freely than short wave radiation. Geiger cautions, however, that varying physical properties can alter this considerably. There have even been occasions when more blue or violet light was transmitted, but this is apparently the result of unusually wet snow having fallen. While this may not be of direct significance, it leads one to suspect that more of the stimulatory short wave lengths may be transmitted by the weathered, melting snow commonly associated with the approach of spring. This suspicion is given strength by Geiger's observation that for old and wet snow, the albedo value drops (from the value of 75 to 100% for new snow) to a value of only 43%. This is in keeping with the observation in the present study that depths of snow which, in the fall, eliminated all light within the selenium cell's sensitivity range were much less effective in reducing light in the spring.

It should also be noted that the insulatory ability of snow similarly decreases as it becomes more weathered and dense. In short, old snow seems to be more transparent than new to cold and to visible solar radiation.

From Geiger's reports, and from observations by several

limnologists (i.e., Nees and Bunge, 1957, and Kalatin, 1951, state that "10 to 15 centimeters of snow absorbs more than 99% of the solar radiation"), one would expect that snow should prevent the major portion of the atmospheric light from reaching small mammals in the subnivean environment. It is clear from the present study that most, if not all, visible light is indeed absent from this environment. In the present study, the light station which showed the greatest decrease in light and the most abrupt increase in spring (station #2 - poplar forest) was in fact the preferred habitat for C. gapperi. However, the total range of C. gapperi is probably better characterized by station #3 (spruce forest), although the vole is thought to probably avoid the "snow shadow" under the spruce trees (Pruitt, 1957). The records from station #3 are conservative, therefore, from the point of view of these rodents.

The present study also indicates the enormous magnitude of the spring light increase which is caused by melting of the snow cover. It is again emphasized that this variant is operating while food and temperature have not yet changed appreciably in the microclimate of the voles, and that the magnitude of the light intensity change and its abruptness is probably greater than is ever observed with respect to the latter two variants. It might be said, therefore, that because snow enhances the nature and the value of the spring increase in light intensity and photoperiod, light is of greater importance as a stimulant to subnivean mammals than to those living above the snow.

Despite the obvious potential of light as a stimulant

to breeding, and the evidence that many mammals do react to it, it is well to caution against the assumption that all mammals would follow suit. Tropical mammals, such as the guinea pig, do not appear to be affected by light changes, as would be expected of a species living under conditions of almost constant day length and, more important, continuously optimal breeding conditions (Dempsey, et al., 1934). Although it is open to question, there is evidence that some subterranean mammals (i.e., ground squirrels) are not stimulated by light (Moore et al., 1934). Recently, it has been suggested that the most northern representatives of wide ranging species may rely entirely on endogenous rhythms for their breeding behavior, or may breed continuously (Schwartz, 1963). Schwartz claimed that tundra microtines breed at the same calendar date as their more southern relatives, irrespective of environmental conditions.

Using as an example the lemming, he reported that they normally breed well before the snow is gone, and before any environmental stimulant could act (translation):

It is very important to note that changes of temperature or light conditions cannot be considered factors stimulating the beginning of reproduction in rodents. The length of the day is just beginning to increase, and certainly cannot influence the course of the physiological processes of animals which lead a subnivean way of life. Temperature conditions remain practically unchanged at the time.

In this way, the spring reproduction of subarctic rodents begins not only before the "spring of warmth" but also before the "spring of light".

He goes on to suggest that the situation may be similar with tropical mammals, where the environmental meteorological conditions are so similar throughout the year that there is no need for a distinct breeding season, and draws an analogy between the continuously-breeding tropical mammals and the lemmings which "practically retain their sexual potency during the whole year". There may well be a trend, then, for these animals in a relatively constant environment to retain their sexual potency throughout the year.

With respect to other microtines, which do not approach continuous breeding but which breed as early as their southern relatives, we might assume that there is no longer any evolutionary advantage to a distinct breeding season and that summer is no more optimal for raising young than winter or spring. One wonders, however, why this apparently advantageous quality of being able to reproduce successfully regardless of the season has not developed in more southern forms as well.

The 1963 essay of Schwartz leaves some question open, however, as to whether he has fully realized all meteorological changes which may occur. He concedes, for instance, that light has begun to increase before lemmings (and other northern microtines) usually begin to breed under the snow, but states that in the subnivean environment they would be denied any knowledge of this change (see quotation above). In his words, "The days get markedly longer but snow still covers the tundra

with a compact cover and the rodents lead a typically winter, subnivean way of life". While this may possibly be true under taiga conditions, it is unlikely that tundra snow depths are usually great enough to exclude all light from the subnivean environment.

Schwartz cites no data on the actual subnivean light levels. Furthermore, the very fact that it is a "compact cover" of snow would certainly affect the light penetrance of snow even if adequate depths were present. Even in the present parkland study, the weathering and compacting of the snow in February and March resulted in a considerable increase in light penetration.

One wonders too what effect the shortening of daylight hours in the fall may have on far northern mammals. Many birds are known to require a period of short day length in order to breed in the following year (Farner, 1964). Some mammals, such as sheep (Hafez, 1959) are able to respond to decrease rather than increase in illumination (however, these are fall breeders). Certainly all northern microtines would be exposed to the phenomenon of decreasing daily photoperiod annually, and one cannot rule out the possibility of some effect.

Even assuming that certain northern mammals may rely on an inherent rhythm of some sort for the annual breeding cycle, it still cannot be inferred, as Schwartz apparently has, that meteorological events have no importance. For in fact, litter size itself, which Schwartz admits is extremely important in the success of lemming populations, has been shown to be affected by illumination. Baker and Ransom (1932), working

with Microtus agrestis, and Pinter and Negus (1965), working with Microtus montanus have shown litter sizes to be significantly larger in animals experiencing long day length (15L/9D) than in those under short day conditions (9L/15D). In mustelids (short-tailed weasel (Mustela erminea), pine marten (M. americana) and mink (M. vison)) the effect of increased illumination is to shorten the gestation period by almost one hundred days by reducing the delay in implantation. In view of these facts, I do not feel that Schwartz is fully justified in suggesting that reproduction in far northern microtines is isolated from the effects of the physical environment.

With respect to the concept of an inherent reproductive rhythm, I should first point out that the reliability of this supposed factor is still open to question, being at best erratic in ferrets (some animals did not breed for two years without light, and some not at all) and incompletely studied in voles. But assuming it exists, it apparently can be overridden by the stimulus of light. This ensures that, should snow disappear earlier than usual (and light therefore increase earlier than usual), the animals could commence breeding immediately and quite possibly succeed in raising an extra litter during the extended breeding season.

It is probably significant that all birds and mammals which have exhibited an internal rhythm in the absence of light change have become mature at a time later than would occur in nature. Therefore the ability to speed breeding may well be an important effect of light, especially when one considers the tremendous increase in total population that could be

realized by the production of one extra litter in a given year.

It would appear that such an extension of breeding season could be achieved by a premature snow melt. This would simulate the increase in illumination associated with the approach of spring.

There is one more phenomenon observed in microtine rodents to which snow and light may have some relevance. This is the occasional observation of winter breeding, beneath the snow.

It has already been suggested that food and temperature may often be favorable enough to permit winter breeding, were sexual development somehow stimulated. Lecyk (1963) feels that the effect of light is especially marked in the autumn-winter period, with internal factors providing the necessary impetus in the spring. In this view, an unusual increase in light during this autumn-winter period could stimulate breeding. Such a "premature" stimulus could result from unusual modification of the snow cover.

Two factors could conceivably contrive to modify snow in such a way as to simulate an increase in light similar to that encountered in spring. These factors are:

- 1) - alteration in snow depth by wind movement.
- 2) - change in physical attributes through weathering (i.e., increase in density brought about by compacting and possibly melting of snow.

It is also possible that circumstances might alter behavior and so cause animals to expose themselves to atmospheric light (and temperatures). In view of their avoidance of light in laboratory experiments, this possibility seems unlikely.

Both of the enumerated phenomena were observed during the course of the current study. Wind drift accounted for the great buildup of snow at the poplar station and the retention of it there. Meanwhile there was a corresponding decrease of snow in the open clearing (this effect may have been even more pronounced in more open areas which allow more wind action). Secondly, as spring approached and atmospheric temperatures rose above the freezing point, the snow cover appeared to lose some of its ability to block the passage of light.

These phenomena were most pronounced in the open fields, which are frequented by Microtus pennsylvanicus. The reader is referred to Figure 13, which shows a considerable increase of light at the open clearing station in mid-February, due apparently to the factors suggested. One wonders if such an increase might not stimulate gonad development in animals inhabiting this environment. In view of this question, it is interesting that plague numbers of M. pennsylvanicus occurred in the vicinity of Edmonton (including the study area) in the spring of 1966, with the small size of many of the animals suggesting strongly that they were born during the winter. This is somewhat reminiscent of the work of Hamilton (1937) in which he observed increases in the M. pennsylvanicus population during winters of low snow in the state of New York.

The photosensitivity of mammals in general has been amply documented. Moreover, many of the photosensitive animals are microtine rodents which spend part of their yearly existence under a protective layer of snow. This study demonstrates that under parkland conditions, it is not the annual change in the

position of the earth relative to the sun, but rather the decrease in snow depth which is responsible for the phenomenon of light increase. Besides the possibility of synchronizing a supposed inherent breeding rhythm and contributing to the reproductive success of the mammals, it is possible, under the conditions described, for premature information to be communicated to the subnivean mammals, causing unseasonal breeding (i.e., winter breeding or early spring breeding). Since both the time of breeding and the size of litters produced are influenced by light and are of importance to the reproductive success of a microtine population, these may also play roles in the fluctuations in numbers of these animals. It may be, therefore, that snow has more significance than has been suspected with regard to the success of northern rodents.

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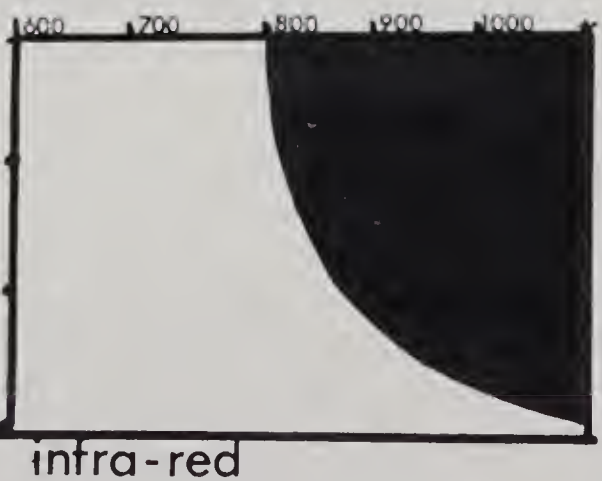
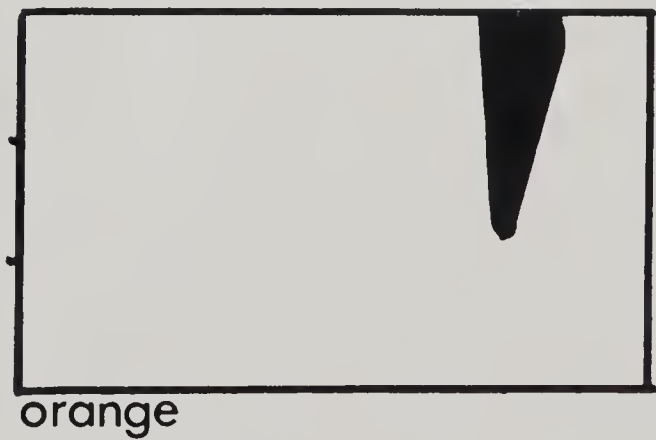
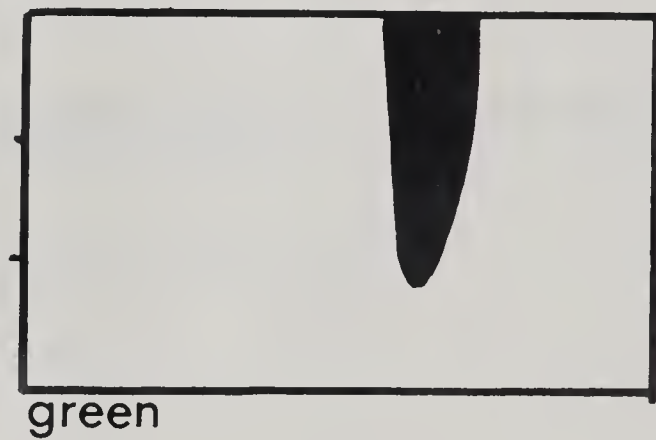
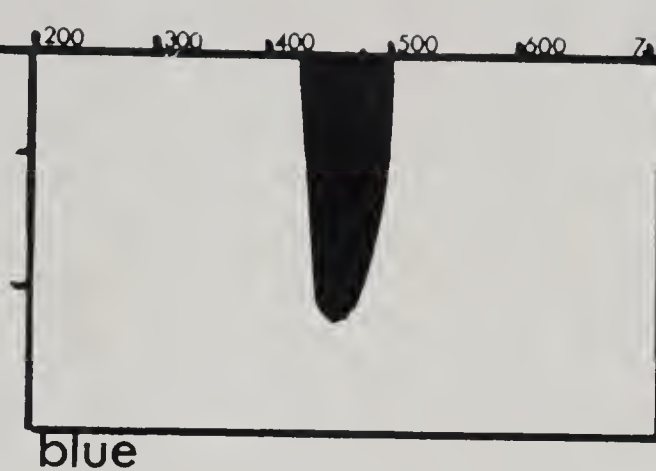
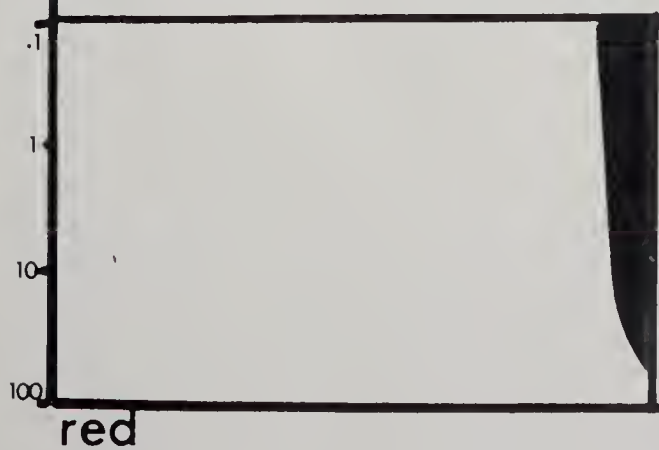
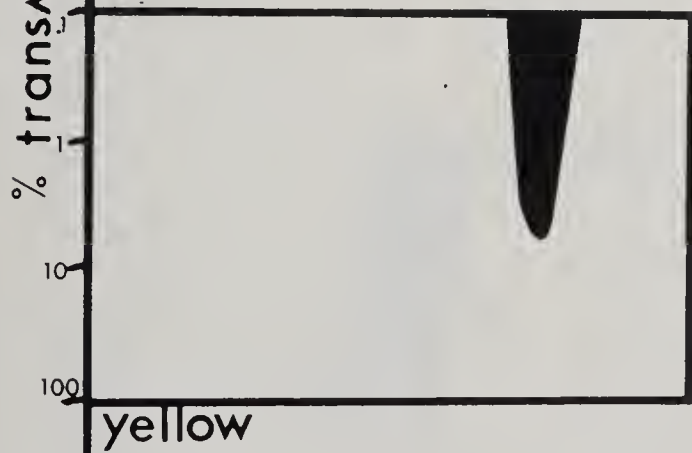
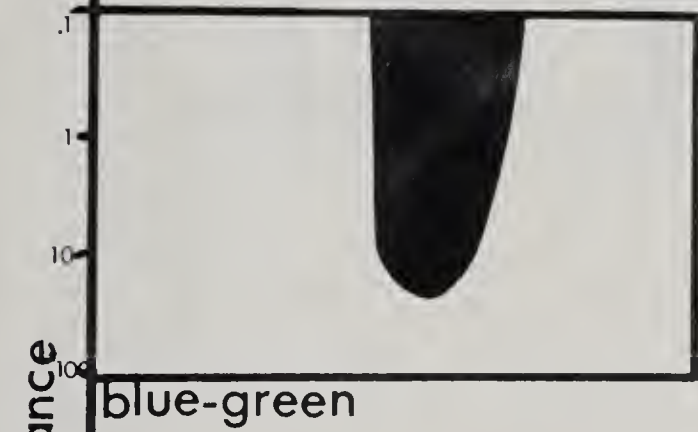
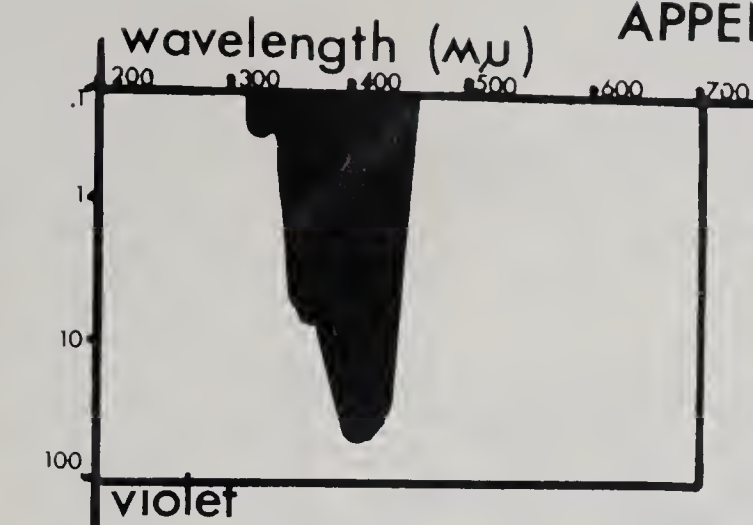
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A P P E N D I C E S

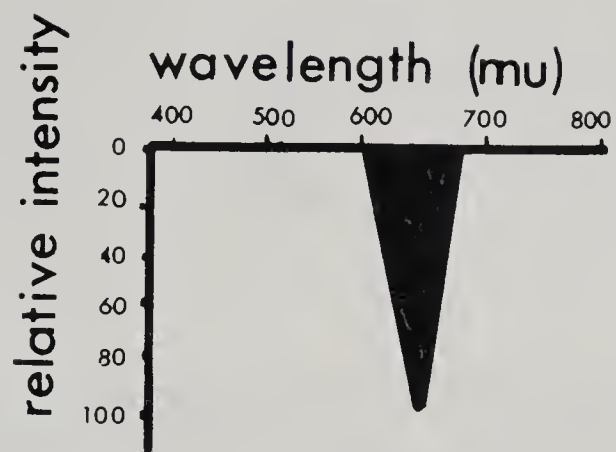
Appendix I. Transmittance curves for Kodak Wratten filters used in color preference experiments.

APPENDIX #1

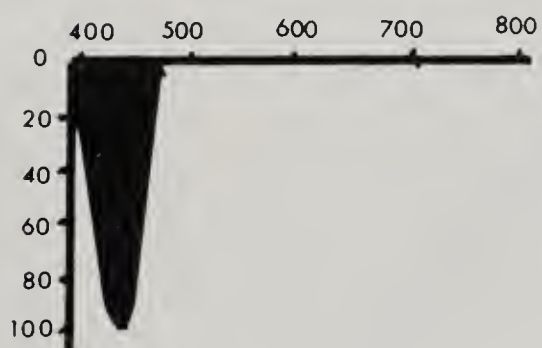


Appendix II. Transmittance curves for CBS filters used
in wave length experiments.

APPENDIX #2



RED FILTER # 650



BLUE FILTER # 450

Appendix III. A rough calibration from milliamperes to foot-candles and lux for selenium photo-cells used in this study.

APPENDIX #3

